

# Energy Considerations in the Bay of Fundy System<sup>1</sup>

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## ABSTRACT

Following developments of Taylor, Allard and Redfield, the rates at which energy is dissipated in the Bay of Fundy in various ways are calculated. A total of  $30.9 \times 10^6$  kw. is transmitted into the bay, of which  $1.26 \times 10^6$  kw. is transmitted into Passamaquoddy Bay. Work is done on the moon at the rate of  $2.48 \times 10^6$  kw. and  $0.03 \times 10^6$  kw. is used to maintain the mixed state in the waters of the Bay of Fundy. The remaining  $27.1 \times 10^6$  kw. must be dissipated by tidal friction. This value is compatible with the usual concepts of turbulent flow over a rough surface if the "roughness length" ( $Z_0$ ) is equal to 0.4 cm. or the average size of the roughness elements ( $E$ ) is about 11 cm.

The effect which the extraction of additional power from the system would have on tidal ranges is evaluated. The range at the head of the Bay of Fundy would decrease at the rate of 0.84 foot (26 cm.) for each million kilowatts. The proposed Passamaquoddy Project would probably increase the mean tidal range at Hopewell Cape by 0.6 foot (18 cm.)

## INTRODUCTION

MUCH HAS BEEN WRITTEN concerning the tides in the Bay of Fundy. For long they have been called "the greatest tides in the World" (Marmer, 1926, p. 217), referring to the range from low water to high water, which at springs may be as great as 50 feet (15 m.) at the head of the bay.

The extreme ranges are attributed to the fact that the bay is of physical dimensions appropriate to make it a quarter-wave resonator whose natural period is close to the period of the semi-diurnal tide ( $M_2$ ). This is confirmed by analysis of the data on the tidal wave. The characteristics of a standing wave are exhibited to a large degree. Redfield (1950) has made an analysis of these tides and confirms the existence of a near-resonance condition. This alone, he shows, does not make the Bay of Fundy unique. The extreme range, according to the analysis, results from the near-resonant system being driven by the tidal wave in the Gulf of Maine which has already been augmented to give a mean amplitude of approximately 9 feet (2.7 m.).

The energy involved in ocean tides is tremendous and there has been much speculation upon, and experimentation with, methods by which useful power might be extracted for man's use. The possibilities seem particularly good in the Fundy area where the large ranges suggest the establishment of an hydraulic head sufficient for practical development of electric power. A scheme for such a development in the Passamaquoddy Bay region was drawn up in some detail and extensively studied in the early 1930's. A re-survey of this project is currently being carried out. There are also projects envisaged for the head of the Bay of Fundy which are actively promoted from time to time.

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In considering the extraction of power from a tidal system, it is prudent to consider the probable effect upon the system itself. This is particularly true for a system which owes its characteristics to a resonance phenomenon. The extraction of energy from the system will change the conditions of resonance. Hachey (1934) made an elementary analysis of this problem as related to the Passamaquoddy Project. He concluded that the project would increase the spring range of the tide by as much as 0.85 ft. (26 cm.) at the head of the Bay of Fundy.

Considerable energy is dissipated in the Bay of Fundy by tidal friction and other phenomena. The result is a damping of the tidal wave. Redfield (1950) introduced a damping term into his analysis of the form  $e^{-\mu x}$ , where distance  $x$  is measured in terms of the actual wavelength. He evaluated a damping coefficient  $\mu$  approximately equal to 1; that is, the wave is attenuated to 0.78 of its amplitude in travelling from the head of the bay to the nodal line (one-quarter wavelength). Appreciable augmentation in amplitude is not to be expected towards the head of a resonant bay where  $\mu$  is greater than about 3.

At the time of writing, an extensive re-survey of the Passamaquoddy Project is being carried out to determine whether it is economically feasible and desirable to extract electric power from the tides at this location. For this reason, it seems appropriate to consider in some detail the various ways in which energy is dissipated in the Bay of Fundy and to evaluate the power involved.

# 1. TRANSMISSION OF ENERGY INTO THE BAY OF FUNDY

## (A) THEORY

Consider the passage of energy through plane (P) (Fig. 1) associated with a tidal wave.  $\xi$  is the instantaneous tidal height above mean water level which is a distance  $h$  above the bottom.  $V$  is the instantaneous particle velocity.

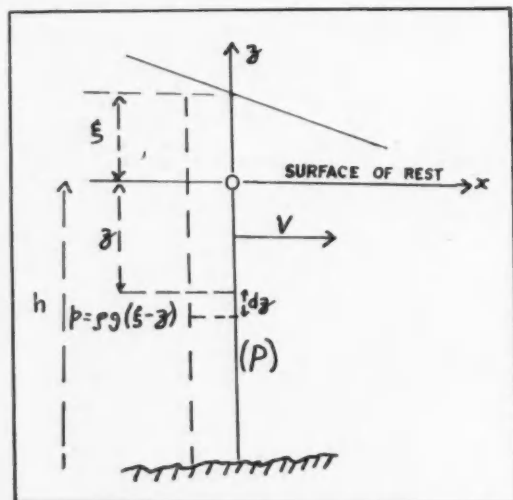


FIG. 1.

The rate at which work  $W$  is being done on the plane is given by

$$W = b \int_{-h}^{\xi} p V dz \quad 1.01$$

where  $b$  is the width of the plane and  $p$ , the pressure, is given by  $p = \rho g(\xi - z)$ ,  $\rho$  being density and  $g$  the acceleration of gravity.

If the depth ( $h$ ) of water below the mean surface level is large compared to the amplitude  $\xi_0$  of the wave it may be considered that  $\xi$  and  $V$  vary sinusoidally, that the area  $A$  of the plane varies little from a mean value  $A = bh$ , and, to a sufficient approximation,

$$W = A V \rho g (\xi + h). \quad 1.02$$

$\xi$  may be written

$$\xi = \xi_0 \cos \frac{2\pi}{T} (t - t_H) \quad 1.03$$

where  $T$  is the period of tidal oscillation and  $t_H$  is the time of high water ( $\xi = \xi_0$ ).

Likewise  $V$  may be written

$$V = -V_0 \sin \frac{2\pi}{T} (t - t_s) \quad 1.04$$

where  $t_s$  is the time of high-water slack and  $V_0$  is the maximum current ( $V$  positive during flooding tide).

Writing  $t_s = t_H + \delta$  and  $t' = (t - t_H)$ , 1.03 and 1.04 become

$$\xi = \xi_0 \cos \frac{2\pi t'}{T} \quad 1.05$$

and

$$V = -V_0 \sin \frac{2\pi}{T} (t' - \delta). \quad 1.06$$

The mean rate at which work is done on the plane, or the mean power transmitted through the plane is:

$$\overline{W} = \frac{A\rho g}{T} \int_0^T V \xi dt \quad 1.07$$

since the mean value of  $V$  is zero. Combining 1.05, 1.06 and 1.07,

$$\overline{W} = -\frac{A\rho g \xi_0 V_0}{T} \int_0^T \cos \frac{2\pi}{T} t' \sin \frac{2\pi}{T} (t' - \delta) dt$$

which yields

$$\overline{W} = \frac{A\rho g \xi_0 V_0}{2} \sin \frac{2\pi}{T} \delta. \quad 1.08$$

There will be no net transport of energy when high water occurs simultaneously with high-water slack ( $\delta = 0$ ).  $\overline{W}$  will be a maximum when high-water slack occurs a quarter of a period after high water ( $\delta = \frac{T}{4}$ ).

The variation in power ( $\bar{W}$ ) with the phase relationship between velocity ( $V$ ) and elevation ( $\xi$ ) is illustrated in Fig. 2 (after Allard, 1953).

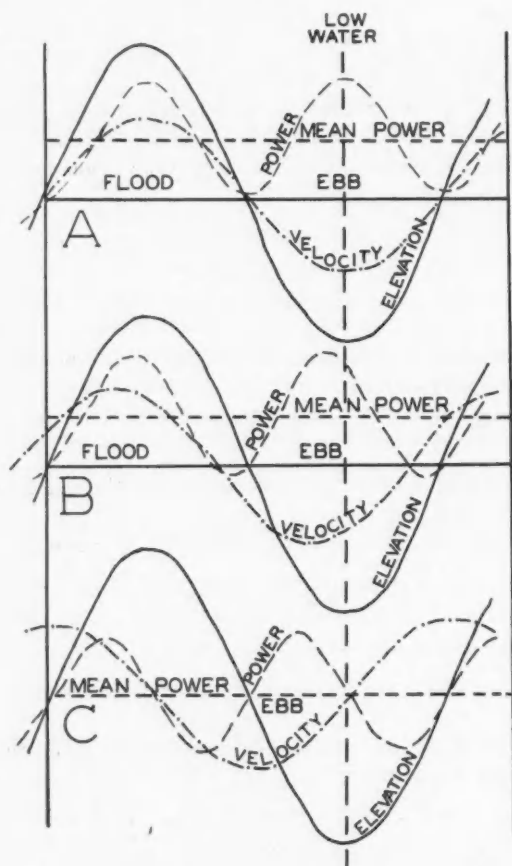


FIG. 2. Variation in mean energy transport (power) with phase relationship between velocity and elevation. (after Allard).

- A. Velocity and elevation in phase (high-water slack  $T/4$  after high water).
- B. Velocity leads elevation by 1 hour (high-water slack  $T/6$  after high water).
- C. Velocity leads elevation by  $T/4$  (high-water slack coincides with high water).

#### (B) APPLICATION TO THE BAY OF FUNDY

For the purpose of evaluating energy parameters in the Bay of Fundy, the bay has been enclosed by an arbitrarily chosen line running from Dennison Point, Maine, ( $44^{\circ}38.5' \text{ N.}$ ,  $67^{\circ} 14.5' \text{ W.}$ ) to Cape St. Mary, Nova Scotia, ( $44^{\circ}05' \text{ N.}$ ,



66°12.5'W.). This is shown in Fig. 3. The line is 55.7 nautical miles (103 km.) in length and the mean chart depth along it is 29.2 fathoms (53.3 m.). It will be necessary to assign values to  $A$ , the area of cross-section,  $\xi_0$ , the tidal amplitude,  $V_0$ , the maximum tidal velocity, and  $\delta$ , the time from high water to high-water slack.

The mean tidal ranges from stations located close to the chosen boundary are given in the following tabulation. The values have been taken from published tide tables of the U.S. Coast and Geodetic Survey and locations of stations are shown on Fig. 3.

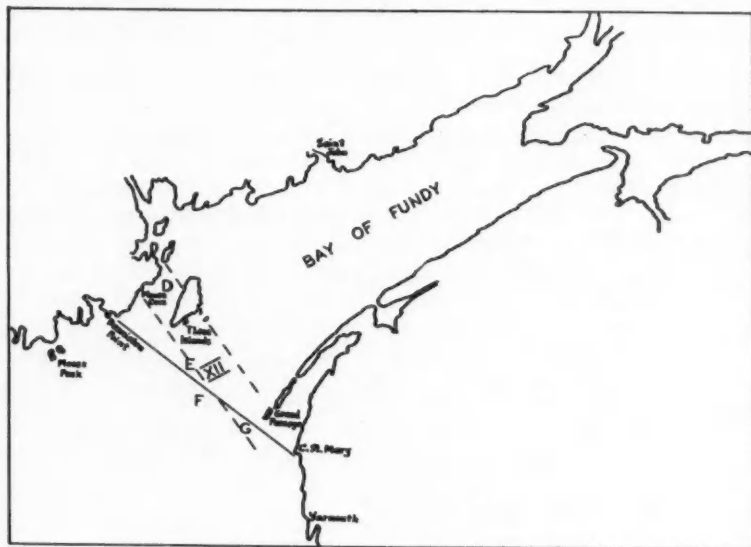


FIG. 3. The Bay of Fundy showing line arbitrarily chosen as mouth of bay, location of current stations and of Ketchum's Section XII.

Station	Mean Range feet
Moose Peak Light	13.9
Grand Passage	14.7
Yarmouth	10.5
Moose Cove	14.8
Three Islands	14.4

A value of 14.2 feet is taken as a reasonable estimate of the mean tidal range at the chosen boundary.  $\xi_0 = 7.1$  feet = 2.16 m.

Dawson (1908) made series of current observations at a number of locations within the Bay of Fundy. The location of his Stations D, E, F and G near the chosen boundary are shown in Fig. 3. He reported maximum flood and ebb currents adjusted to the mean tidal range. These values plus their average values are tabulated as follows.

Station	Maximum current strength		
	Flood <i>knots</i>	Ebb <i>knots</i>	Average <i>knots</i>
D	2.65	2.15	2.40
E	2.65	3.90	3.28
F	1.40	1.20	1.30
G	2.70	2.50	2.60
Mean: 2.39			

Ketchum and Keen (1953), in studying the flushing, segmented the Bay of Fundy according to mean tidal excursions which they computed on the basis of the volume of water introduced as the tide floods. Their Section XII, between the dashed lines on Fig. 3, had a length of 9.0 nautical miles (16.7 km.) which requires a mean velocity of  $\frac{9.0}{6.2} = 1.45$  knots (74.6 cm. sec.<sup>-1</sup>). This mean velocity

would require a maximum velocity ( $V_0$ ) of  $\frac{\pi}{2}$  times the mean, or  $V_0 = \frac{\pi}{2} \times 1.45 = 2.28$  knots.

A value of  $V_0 = 2.3$  knots = 118 cm. sec.<sup>-1</sup> is therefore reasonable.

Redfield (1950) has reported certain values for the time angle between high water and slack water at some of Dawson's (1908) stations. He related the current data to tidal height data from a neighbouring shore station and reported the difference between the Greenwich hour angles for slack water ( $G_s$ ) and for high water ( $G_h$ ). These values he compared to theoretical figures derived from his analysis of the system of tides in the bay as a whole. The theoretical figures are reported as

$$-(\sigma t_H - \sigma t_s) = -\left(\frac{2\pi}{T} t_H - \frac{2\pi}{T} t_s\right) = \frac{2\pi}{T} \delta$$

in the nomenclature herein used.

Current station	Reference station for high water	Time angle between high water and slack water	
		Data $G_s - G_H$	Theory $-(\sigma t_H - \sigma t_s)$
D	Moose Cove	21°	26°
E	Three Islands	24°	23°
G	Grand Passage	31°	27°

The agreement is good considering the short periods for which data were available for analysis and the way in which the theoretical model of the bay was fitted to the prototype.

A respectable figure for  $\frac{2\pi}{T} \delta$  at the chosen boundary (Fig. 3) would be 25°.

It has already been stated that the boundary section is 103 km. long and has a mean chart depth of 53.3 m. Adding  $\xi_0 = 2.16$  m. to the chart depth to arrive at a mean depth of water gives for the area of cross-section

$$A = 5.72 \times 10^6 \text{ m.}^2.$$

Equation 1.08 may now be entered with the following values for the various parameters:

$$\begin{aligned} A &= 5.72 \times 10^{10} \text{ cm.}^2 & V_0 &= 118 \text{ cm. sec.}^{-1} \\ \rho &= 1.025 \text{ gm. cm.}^{-3} & \xi_0 &= 216 \text{ cm.} \\ g &= 980 \text{ cm. sec.}^{-2} & \frac{2\pi\delta}{T} &= 25^\circ, \end{aligned}$$

giving

$$\begin{aligned} \overline{W} &= 3.09 \times 10^{17} \text{ ergs sec.}^{-1} \\ &= 30.9 \times 10^6 \text{ kw.} \end{aligned}$$

#### (C) APPLICATION TO PASSAMAQUODDY BAY

The U.S. Coast and Geodetic Survey publish tables from which the time of slack water can be computed for Western Passage, off Kendall Head (Fig. 4). The flood interval is given as 9 hours 25 minutes, which would give a high-water slack interval  $9:25 + 3:06 = 12$  hours 31 minutes. The high-water interval at Eastport, Maine, is 11 hours 07 minutes, so that

$$\delta = 1 \text{ hour } 24 \text{ minutes} = 1.40 \text{ hours.} \quad \frac{2\pi\delta}{T} = 41^\circ.$$

The tables give for the mean velocity at strength of flood off Kendall Head  $V_0 = 3.1$  knots  $= 160 \text{ cm. sec.}^{-1}$ . The mean tidal range at Eastport is 18.2 feet,  $\xi_0 = 9.1$  feet  $= 2.77$  m. The cross-section of Western Passage off Kendall Head has a width of 1.36 km. and a mean chart depth of 111 feet (33.8 m.). Adding 9 feet for  $\xi_0$  gives a mean depth 120 feet (36.6 m.) and  $A = 4.98 \times 10^8 \text{ cm.}^2$ . Equation 1.08 is entered with

$$\begin{aligned} A &= 4.98 \times 10^8 \text{ cm.}^2 & \xi_0 &= 277 \text{ cm.} \\ \rho &= 1.025 \text{ gm. cm.}^{-3} & V_0 &= 160 \text{ cm. sec.}^{-1} \\ g &= 980 \text{ cm. sec.}^{-2} & \frac{2\pi\delta}{T} &= 41^\circ, \end{aligned}$$

giving

$$\begin{aligned} \overline{W} &= 7.3 \times 10^{15} \text{ ergs sec.}^{-1} \\ &= 7.3 \times 10^5 \text{ kw.} \end{aligned}$$

The cross-section area of Letite Passage has been calculated from echo-sounder traces taken by W. G. Carson from M. B. *Mallotus* at low water slack on May 19, 1952. Two sections at different points in the passage each gave  $A = 3.6 \times 10^8 \text{ cm.}^2$ .

There are no reliable values for current velocities or for the phase relation between high water and slack water. The velocities are probably somewhat higher than in Western Passage and the phase angle is probably closer to the value of  $25^\circ$ .

which Redfield gives for the vicinity of Lepreau Bay. If the assumption is made that the energy flux is in proportion to the areas of cross-section,

$$\overline{W} = \frac{3.6}{4.98} \times 7.3 \times 10^5 = 5.3 \times 10^5 \text{ kw.}$$

This is probably a fair approximation.

Thus the estimated total energy flux into Passamaquoddy Bay is

$$7.3 \times 10^5 + 5.3 \times 10^5 = 1.26 \times 10^6 \text{ kw.}$$

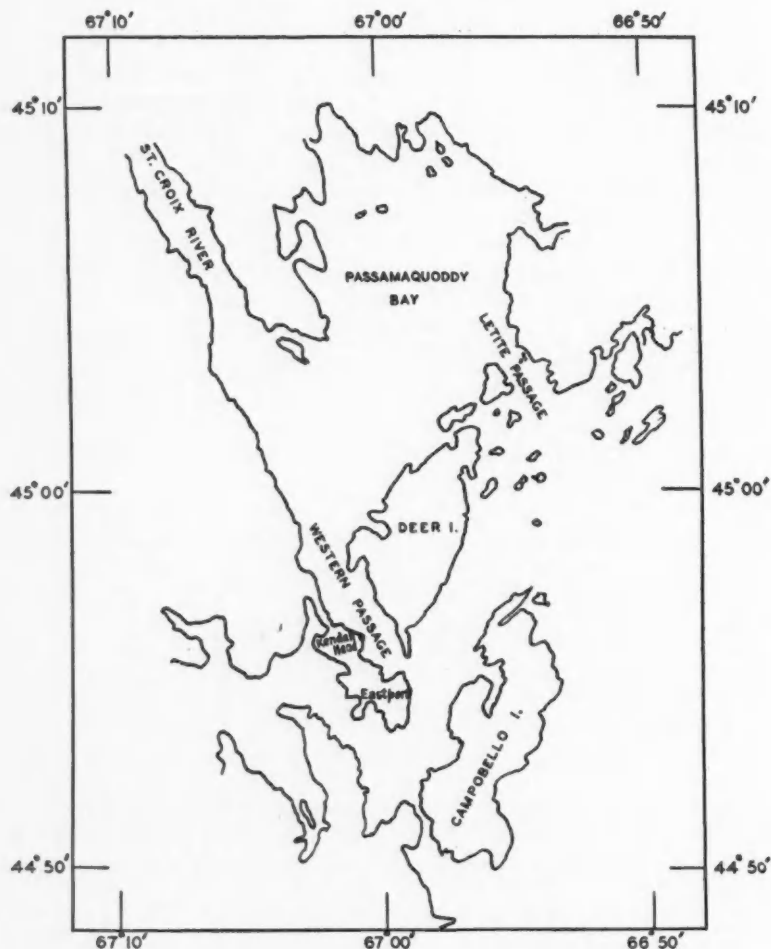


FIG. 4. Chart of Passamaquoddy Bay and connecting passages.

## 2. WORK DONE BY THE MOON ON THE BAY OF FUNDY

Taylor (1919) has given a development showing how the work done by the moon on a body of water subjected to tides may be calculated. He gives

$$W_m = -\frac{3}{2} \frac{\pi \rho \xi_0}{2T} \left( \frac{\gamma E}{R^2} \right) \left( \frac{M}{E} \right) \left( \frac{R^3}{D_m^3} \right) R \cos^2 \lambda \sin 2\Phi_0 \quad 2.01$$

where

$W_m$  = mean rate at which work is done by the moon's attraction per unit area

$\rho$  = density

$\xi_0$  = amplitude of tidal wave (half the range)

$T$  = the period of the semi-diurnal tides

$\gamma$  = the gravitational constant

$E$  = mass of the earth

$R$  = radius of the earth

$M$  = mass of the moon

$D_m$  = radius of the moon's orbit

$\lambda$  = latitude of the place

$\Phi_0$  = the phase of the tide at the time when the moon crosses the meridian (in Taylor's development, this is half the phase angle of the semi-diurnal tide).

Now  $\frac{\gamma E}{R^2}$  is the attraction of the earth at its surface

$$\frac{\gamma E}{R^2} = g = 980 \text{ cm. sec.}^{-2}$$

$$\frac{M}{E} = \frac{1}{81}$$

$$\frac{R}{D_m} = \frac{1}{60}$$

$$R = 6.4 \times 10^8 \text{ cm.}$$

$$T = 4.47 \times 10^4 \text{ sec.}$$

$$\rho = 1.025$$

$$\begin{aligned} W_m &= -\frac{3\pi \times 1.025 \times 980 \times 6.4 \times 10^8}{4 \times 4.47 \times 10^4 \times 81 \times 60 \times 60 \times 60} \xi_0 \cos^2 \lambda \sin 2\Phi_0 \\ &= -1.94 \xi_0 \cos^2 \lambda \sin 2\Phi_0 \text{ ergs cm.}^{-2} \text{ sec.}^{-1} \end{aligned} \quad 2.02$$

if  $\xi_0$  is in centimetres.

Taking  $\lambda = 45^\circ$  as a mean figure for latitude in the Bay of Fundy

$$\cos^2 \lambda = 0.50$$

$$W_m = -0.97 \xi_0 \sin 2\Phi_0 \text{ ergs cm.}^{-2} \text{ sec.}^{-1}. \quad 2.03$$

At Saint John, N.B., ( $45^{\circ}15'N.$ ,  $66^{\circ}04'W.$ ) the high water follows the moon's meridional passage by 11 hours 09 minutes (W. J. Farquharson's personal communication), or 11.15 hours; that is, the previous high water precedes the moon's passage by 12.42–11.15 hours. Relative to high water, the phase angle of the semidiurnal tide is

$$\frac{12.42-11.15}{12.42} \times 360^{\circ} = +36.8^{\circ} \text{ hence } \Phi_0 = +18.4^{\circ}.$$

For each of 21 tidal stations, the phase angle was calculated using a correction in time to the Saint John tides from existing tables, and a correction for the difference in longitude. The product  $\xi_0 \sin 2 \Phi_0$  was calculated for each station. These values, shown in Table I, were plotted on a chart of the area and interpolated values assigned to each  $10'$  rectangle. These were then averaged for the whole area, giving

$$\text{average } \xi_0 \sin 2 \Phi_0 = 178 \text{ cm.}$$

The area of the Bay of Fundy enclosed by the chosen outer boundary and excluding Passamaquoddy Bay is  $1.44 \times 10^{14} \text{ cm.}^2$

$$\begin{aligned} W_m &= -0.97 \times 178 \times 1.44 \times 10^{14} \\ &= -2.48 \times 10^{16} \text{ ergs sec.}^{-1} \\ &= -2.48 \times 10^6 \text{ kw.} \end{aligned}$$

Since high water occurs slightly before the moon's meridional passage, the bay does this amount of work on the moon. A similar condition was found by Taylor (1919) to obtain for the Irish Sea.

It is of interest to note in Table I the value of parameters recorded for the stations Burntcoat Head and Horton Bluff. The time lag occasioned in traversing the narrow entrance to Minas Basin, coupled with the longitude correction, reduces the phase angle of the semi-diurnal tide to a very small value. Here, where the greatest tidal ranges of all occur, the surface elevation is in phase with the tide-generating potential. Elsewhere in the bay the lunar tidal forces act to inhibit the oscillation.

### 3. ENERGY USED IN MIXING

One of the characteristic features of the Bay of Fundy is the comparative lack of vertical stratification. This homogeneity is attributed to the action of the tides in bringing about intense vertical mixing. An estimate will be made of the power involved in maintaining the mixed state.

#### (A) THEORY

The potential energy per unit area in a column of water of depth  $H$  can be written

$$\text{P.E.} = \int_0^H \rho g h dh \quad 3.01$$

where  $\rho$  is the density,  $g$  the acceleration of gravity, and  $h$  the height measured from the bottom ( $h = 0$ ) to the surface ( $h = H$ ).

TABLE I. Calculation of  $\xi_0 \sin 2\Phi_0$  for tide stations in the Bay of Fundy.

Station	Latitude		Longitude		Phase of the semi-diurnal tide	Sin $2\Phi_0$	$\xi_0$ cm.	$\xi_0 \sin 2\Phi_0$ cm.
	N.	'	W.	'	hours			
	°	'	°	'	hours	°( $2\Phi_0$ )		
Grindstone Island	45	43	64	37	+0.42	0.75	.368	176
Quaco	45	20	65	32	+0.22	1.01	.450	152
Saint John	45	15	66	04	0	1.27	.599	158
Lepreau Bay	45	07	66	29	-0.05	1.35	.630	177
L'Etang Harbour	45	02	66	49	-0.03	1.35	.630	169
Welchpool	44	53	66	57	-0.18	1.81	.689	192
West Quoddy Head	44	49	66	59	-0.31	1.64	.737	176
Moose Cove	44	44	67	07	-0.32	1.66	.743	168
North Head Grand Manan	44	46	66	45	-0.25	1.57	.711	181
Three Islands	44	35	66	46	-0.46	1.78	.782	171
Moose Peak Light	44	29	67	32	-0.35	1.72	.764	162
Grand Passage	44	16	66	20	-0.53	1.82	.795	179
Burntcoat Head	45	18	63	49	+1.13	+1.15	-.005	600
Horton Bluff	45	06	64	13	+1.08	+0.13	.030	548
Spencer Island	45	20	64	42	+0.37	+0.09	.397	457
Black Rock	45	10	64	46	+0.13	+0.09	.506	421
Isle Haute	45	15	65	00	+0.03	+0.07	.557	402
Port George	45	01	65	01	-0.03	+0.06	.585	387
Digby	44	38	65	45	-0.28	1.24	.657	226
Weymouth	44	27	66	01	-0.43	1.53	.757	208
Petite Passage	44	24	66	13	-0.58	1.70	.807	200
						1.86		189

To evaluate this function approximately from observations of density at discrete serial depths, 3.01 may be written in the form

$$\text{P.E.} = \sum_0^H g \bar{\rho} \bar{h} \Delta h \quad 3.02$$

where  $\bar{\rho}$  is the mean density of water in the interval whose mean height from the bottom is  $\bar{h}$ .

Assume a simple estuary where fresh water of density  $\rho_f$  flows in at the surface over water of a uniform high salinity  $S$  and of density  $\rho_s$ . A fictitious potential energy function (P.E.)' is defined to represent a situation where no mixing had taken place between the two layers:

$$(\text{P.E.})' = \bar{h}_s \Delta h_s \rho_s g + \bar{h}_f \Delta h_f \rho_f g \quad 3.03$$

where  $\Delta h_s$  is the thickness of the salt water layer whose mean height is  $\bar{h}_s$  and  $\Delta h_f$  the thickness of the fresh water layer whose mean height is  $\bar{h}_f$ .

$$\bar{h}_s = \frac{\Delta h_s}{2} \quad 3.04$$

and

$$\bar{h}_f = \Delta h_s + \frac{\Delta h_f}{2}. \quad 3.05$$

Once a base salinity  $S$  has been selected  $\Delta h_s$  can be calculated from the observed mean salinity in the column as actually observed  $\bar{S}$ .

$$\Delta h_s = \frac{\bar{S}}{S} H \quad 3.06$$

and

$$\Delta h_f = H - \Delta h_s = H \left( 1 - \frac{\bar{S}}{S} \right) \quad 3.07$$

3.03 becomes

$$(\text{P.E.})' = \frac{gH^2}{2} \left[ \rho_f + \left( \frac{\bar{S}}{S} \right)^2 (\rho_s - \rho_f) \right]. \quad 3.08$$

The difference between the two potential energy functions 3.02 and 3.03 gives a measure of the amount of energy per unit area which has been expended in producing the mixed state

$$\begin{aligned} \Delta \text{P.E.} &= \text{P.E.} - (\text{P.E.})' = g \left[ \sum_0^H \bar{\rho} \bar{h} \Delta h - \bar{h}_s \Delta h_s \rho_s - \bar{h}_f \Delta h_f \rho_f \right] \\ &= g \left[ \sum_0^H \bar{\rho} \bar{h} \Delta h - \frac{H^2}{2} \left\{ \rho_f + \left( \frac{\bar{S}}{S} \right)^2 (\rho_s - \rho_f) \right\} \right]. \end{aligned} \quad 3.09$$

The power dissipated in mixing the fresh and salt layers together is given by

$$P_m = \frac{\overline{\Delta \text{P.E.}} \times A}{T} \quad 3.10$$

where  $\overline{\Delta \text{P.E.}}$  is the mean value of  $\Delta \text{P.E.}$  over the area  $A$  which is being considered, and  $T$  is the time in which the mixing has taken place.



If  $R$  is the rate at which fresh water is added to the estuary by run off and precipitation, and  $\Delta \bar{h}_f$  the mean thickness of the fictitious fresh water layer over the area  $A$ , the accumulated fresh water is equivalent to the contributions over a period equal to  $A \frac{\Delta \bar{h}_f}{R}$  and the average particle of fresh water has been in the mixing mechanism for half this long. Thus

$$T = \frac{1}{2} \frac{A \Delta \bar{h}_f}{R} \quad 3.11$$

$$P_m = \frac{2 \Delta \text{P.E. } R}{\Delta \bar{h}_f} \quad 3.12$$

(B) APPLICATION TO BAY OF FUNDY (APRIL 1953 SURVEY)

Between March 29 and April 3, 1953, twenty-two oceanographic stations were occupied in a network covering the Bay of Fundy (Fig. 5). The northeastern line crossed the head of the bay at Isle Haute, and the southeastern line ran from Point of Main to Yarmouth.

For each of the 22 stations,  $\Delta \text{P.E.}$  was calculated assuming a base salinity of 32.9‰ for the deep water being added to the system. Values of  $\Delta \text{P.E.}$  ranged from  $5.7 \times 10^6$  ergs  $\text{cm.}^{-2}$  to  $35.0 \times 10^6$  ergs  $\text{cm.}^{-2}$ . This quantity was contoured for the whole bay and the product  $\Delta \text{P.E.} \times A$  found by planimetry between contours. The product was found for the area inside a line stretching from Cape St. Mary to Dennison Point as shown in Fig. 3.

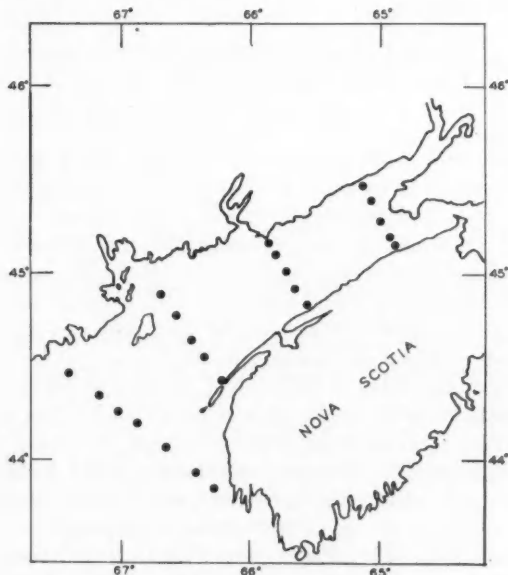


FIG. 5. Stations occupied during cruise S-13. March 29 to April 3, 1953.

The integrated product was

$$\overline{\Delta P.E.} \times A = 2.35 \times 10^{21} \text{ ergs.}$$

These calculations gave a depth for the fictitious fresh water layer varying from 0.55 m. in the centre of the line across the approaches to the bay, to 2.67 m. near the Saint John River estuary. This quantity  $\Delta h_f$  was contoured and the areas between contours were determined by planimeter. The results indicated a total volume of fresh water present equal to  $2.5 \times 10^{10} \text{ m.}^3$ . With a total area  $A = 1.44 \times 10^{10} \text{ m.}^2$ , this gives  $\overline{\Delta h_f} = 1.73 \text{ m.}$

In Table II the monthly mean runoff for the Saint John River as metered at Pokiok is tabulated for the months prior to the survey.

The Saint John above Pokiok has a drainage basin of 15,300 square miles, while the total drainage area of the Bay of Fundy is 31,500 square miles. The runoff figures in second-feet have been multiplied by the factor  $\frac{31.5}{15.3}$  and con-

verted to cubic metres total for each month. Also given are the monthly totals of precipitation recorded at St. Andrews, N.B. These have been converted to cubic metres falling on an area equal to that of the Bay of Fundy to give an approximate figure for the direct contribution of fresh water.

The total contribution of fresh water from the beginning of September 1952 up to the time of survey was  $2.6 \times 10^{10} \text{ m.}^3$ , and the  $2.5 \text{ m.}^3$  total found in the bay represents the contribution of some 195 days.

Half this period represents the average time these waters were in the mixing mechanism so that

$$P_m = \frac{2.35 \times 10^{21}}{97.5 \times 24 \times 3600} = 2.8 \times 10^{14} \text{ ergs sec.}^{-1} = 2.8 \times 10^4 \text{ kw.}$$

### (C) DISCUSSION

The flushing time of 195 days arrived at in these calculations is more than twice that calculated by Ketchum and Keen (1953). This may indicate that there is a significant addition of fresh water to the Bay of Fundy in the flow of low-salinity surface waters around the southwest corner of Nova Scotia during the winter months. That is, the assumption that the bay functions as a simple estuary may not be valid. If fresh water is added by such a mechanism, both computed energy and flushing time will be too large and there will be some compensation in the estimate of mixing power.

Using Ketchum and Keen's (1953) data, which covered mostly the summer months and averaged by 10' rectangles, a rough calculation of mixing power was carried out using their flushing time of 76 days. This gave a figure of  $3.8 \times 10^4 \text{ kw.}$  which is in good agreement with the computed  $2.8 \times 10^4 \text{ kw.}$  for the April 1953 data. Both are in good agreement with Watson's (1936) estimate of  $2.4 \times 10^4 \text{ kw.}$  obtained by an entirely different approach.

In the precipitation and runoff figures (Table II), it is worthy of note that the amount of fresh water contributed directly to the bay by precipitation was

very nearly as great as that from runoff. Ketchum and Keen took no cognizance of the addition from precipitation but used Watson's (1936) figure for the average river flow from April to July inclusive. This may not have been such a serious oversight since the period of maximum runoff and minimum precipitation was considered.

TABLE II. Fresh water contribution to Bay of Fundy by runoff and precipitation during months prior to survey.

Month	Mean runoff Saint John River	Total runoff to Bay of Fundy	Monthly total precipitation St. Andrews	Fresh water con- tribution to Bay of Fundy from precipitation	Runoff plus precipitation
	<i>sec.-feet</i>	<i>m.<sup>3</sup></i>	<i>inches</i>	<i>m.<sup>3</sup></i>	<i>m.<sup>3</sup></i>
March 1953	22,700	$3.52 \times 10^9$	8.14	$2.98 \times 10^9$	$6.50 \times 10^9$
February 1953	13,500	$1.91 \times 10^9$	5.91	$2.16 \times 10^9$	$4.07 \times 10^9$
January 1953	8,940	$1.39 \times 10^9$	5.31	$1.94 \times 10^9$	$3.33 \times 10^9$
December 1952	12,500	$1.95 \times 10^9$	4.76	$1.74 \times 10^9$	$3.69 \times 10^9$
November 1952	14,900	$2.25 \times 10^9$	3.52	$1.29 \times 10^9$	$3.54 \times 10^9$
October 1952	13,000	$2.02 \times 10^9$	2.99	$1.09 \times 10^9$	$3.11 \times 10^9$
September 1952	3,610	$0.55 \times 10^9$	3.42	$1.25 \times 10^9$	$1.80 \times 10^9$
				TOTAL:	$2.604 \times 10^{10}$

#### 4. ENERGY DISSIPATED BY FRICTION

Following the results of Sections 1 to 3, the power budget for the Bay of Fundy system may be summarized as follows:

Transmitted into the Bay of Fundy	$30.9 \times 10^6$ kw.	
Transmitted into Passamaquoddy Bay		$1.26 \times 10^6$ kw.
Work done on the moon		$2.48 \times 10^6$ kw.
Used to maintain mixed state		$0.03 \times 10^6$ kw.
Not yet accounted for		$27.1 \times 10^6$ kw.
	$30.9 \times 10^6$ kw.	$30.9 \times 10^6$ kw.

The  $27.1 \times 10^6$  kw. must be dissipated by friction and escape from the bay in the form of heat.

For turbulent flow in an open channel, the shear stress  $\tau_b$  (tangential force per unit area) exerted by the fluid on the channel bed is generally taken to be of the form

$$\tau_b = \rho \gamma^2 |V| V \quad 4.01$$

where  $\rho$  is the density and  $V$  is the average current velocity in a vertical column.  $\gamma^2$  is a non-dimensional coefficient which depends upon the bottom roughness and the dimensions (depth) of the channel.

The stress is directed parallel to the velocity as is indicated by the use of the product of  $V$  and  $|V|$ , the absolute value of  $V$  without regard to sign.

The rate at which energy is dissipated by friction (per unit area) is the product of stress and velocity

$$\begin{aligned}\frac{dP}{d\sigma} &= \tau_b V = \rho \gamma^2 |V| V^2 \\ &= \rho \gamma^2 |V|^3\end{aligned}\quad 4.02$$

$\frac{dP}{d\sigma}$  is always positive.

Where the flow is tidal in nature  $\gamma^2$  may vary in time for two reasons. Where the tidal amplitude is significant with respect to the mean depth  $\gamma^2$  may vary because of changes in the depth of water. Also, during the parts of the tidal cycle when velocities are low, especially in shallow areas, the assumption of turbulent flow may not be valid.

If these variations in the coefficient  $\gamma^2$  are neglected, and a sinusoidal current assumed, the mean value  $\overline{|V|^3}$  of  $|V|^3$  may be written in terms of the amplitude of tidal current variations  $V_0$

$$\overline{|V|^3} = \frac{4}{3\pi} V_0^3 \quad 4.03$$

so that the time average of  $\frac{dP}{d\sigma}$  is

$$\overline{\frac{dP}{d\sigma}} = \frac{4}{3\pi} \rho \gamma^2 V_0^3. \quad 4.04$$

It remains to evaluate  $\gamma^2$ .

Reid (1957) has developed an equation to represent this coefficient for open channel flow in the absence of surface stress

$$\gamma = \frac{K_0}{\ln\left(\frac{4D}{Z_0}\right)^{-2}}. \quad 4.05$$

$K_0$  is the dimensionless von Karman constant whose value is approximately 0.40 (Rouse 1946, p. 192).  $D$  is the depth of water and  $Z_0$  is a parameter which characterizes the bottom surface.  $Z_0$  is called the "roughness length" and is related to the average size of the roughness elements ( $E$ ). Evaluating  $K_0$  and using base 10 logarithms

$$\gamma^2 = \frac{0.0302}{\left[\log\left(\frac{D}{Z_0}\right) - 0.266\right]^2}. \quad 4.06$$

Kirschmer (1949) and Allard (1953) use an equation similar in form to 4.01 for flow in open channels

$$\tau_b = \rho \frac{\lambda}{2} V^2 \quad 4.07$$

and give for the coefficient  $\lambda$

$$\lambda = \frac{1}{\left[ 4 \log \left( \frac{D}{E} \right) + 4.68 \right]^2} \quad 4.08$$

where  $E$  is the average size of the roughness elements.

The two forms are approximately equivalent if  $E = 27.2 Z_0$ . Both 4.08 and 4.05 hold only for cases where the flow is hydrodynamically rough.

The parameter  $E$  can be evaluated for experimental laboratory studies but not easily for actual conditions in the ocean. Almost unique as reported evaluations of roughness parameters in the oceans are the measurements made by Revelle and Fleming in San Diego Bay (Sverdrup *et al.*, 1942, p. 480). They measured currents at three depths near the bottom and found results compatible with theory only on the basis that the flow was rough and  $Z_0$  had a value 2.0 cm.

Equations 4.04 and 4.06 were used to evaluate the energy dissipated by friction in the Bay of Fundy. The value  $Z_0 = 2.0$  cm. was tried. That portion of the bay inside an arbitrary boundary running from Cape St. Mary to Dennison Point and excluding Passamaquoddy Bay was considered (see Fig. 3).

The area was divided into rectangles of 2' latitude by 2' longitude. To each rectangle a mean depth was assigned from existing charts. Half the appropriate tidal range was added to the chart depth to approximate mean depth of water. The chart so divided was overlain with a chart on which all available current data ( $V_0$ ) had been plotted and contoured. Due to the comparative scarcity of current evaluations this contouring required considerable imagination.

For each rectangle  $V_0$  and  $D$  were then tabulated and  $\rho \gamma^2$  and  $|V|^3$  calculated.

The function  $\frac{d\bar{P}}{d\sigma}$  was then evaluated and integrated over the total area. The value obtained was

$$\begin{aligned} \bar{P} &= 4.13 \times 10^{17} \text{ ergs sec.}^{-1} \\ &= 41.3 \times 10^6 \text{ kw.,} \end{aligned}$$

a value much too large to be compatible with the results of Sections 1 to 3.

A value of  $\bar{P} = 27.1 \times 10^6$  kw. was obtained by using  $Z_0 = 0.4$  cm., just one-fifth of the value arrived at by Revelle and Fleming. This is equivalent to an average size of the roughness elements of approximately 11 cm.

The agreement is good with the results Taylor (1919) obtained in the Irish Sea. He evaluated his frictional coefficient as between  $1.6 \times 10^{-3}$  and  $1.8 \times 10^{-3}$  for a mean depth of 80 m. Equation 4.06, with  $Z_0 = 0.4$  cm., gives  $\gamma^2 = 1.86 \times 10^{-3}$ .

##### 5. POWER, PHASE AND AMPLITUDE

Equation 1.08 relates the power transmitted into the Bay of Fundy to the amplitude  $\xi_0$ , and velocity  $V_0$  of the tidal wave at the entrance and to their

relative phase  $\frac{2\pi\delta}{T}$ . The equation is of the form  $\bar{P} = X \sin \Psi$ . Differentiating,

$$\frac{\partial \bar{P}}{\partial \Psi} = X \cos \Psi \quad 5.01$$

which, evaluated at the chosen boundary, yields

$$\frac{d\bar{P}}{d\Psi} = 1.17 \times 10^6 \text{ kw. per degree phase lag.} \quad 5.02$$

That is, the phase lag would have to increase by one degree if the power transmitted into the bay were to increase by  $1.17 \times 10^6$  kw.

In Redfield's (1950) development the angle  $\Psi = \frac{2\pi}{T} \delta$  is equivalent to  $-(\sigma t_h - \sigma t_s)$ , the difference between the time angles of high and slack water. From his equations 4 and 9b:

$$\Psi = -\tan^{-1}(-\tan kx \tanh \mu x) + \tan^{-1}\left(\frac{\tanh \mu x}{\tan kx}\right) - \tan^{-1}\left(\frac{\mu}{k}\right) \quad 5.03$$

where  $x$  denotes the part of a cycle the wave will complete in passing from a point to the reflecting boundary at the head of the bay,  $k$  is a phase difference of  $360^\circ$ , and  $\mu$  is a damping factor such that  $e^{-\mu x}$  represents the attenuation of the wave in the course of a fraction or multiple of a cycle  $x$ .

Differentiating 5.03 with respect to  $\mu$

$$\frac{\partial \Psi}{\partial \mu} = \frac{x \tan kx \operatorname{sech}^2 \mu x}{1 + (\tan kx \tanh \mu x)^2} + \frac{x \tan kx \operatorname{sech}^2 \mu x}{\tan^2 kx + \tanh^2 \mu x} - \frac{k}{k^2 + \mu^2}. \quad 5.04$$

In the analysis Redfield found best fit between data and theory for  $\mu = 1$ . That is, the wave is attenuated to  $\frac{1}{e}$  of its amplitude in travelling the equivalent of one wave length. The analysis places values on  $kx$  of  $-68^\circ$  and  $\Psi = 25^\circ$  near the line which is here considered as the mouth of the bay.

$$\mu = 1, \quad kx = -68^\circ, \quad k = 2\pi = 360^\circ, \quad x = -0.189,$$

$$\tan kx = -2.47, \quad \tanh \mu x = -0.188, \quad \operatorname{sech} \mu x = 0.984,$$

so that evaluating 5.04

$$\frac{\partial \Psi}{\partial \mu} = 0.51 = 29^\circ. \quad 5.05$$

That is, the phase angle between high and slack waters at the boundary changes at the rate of  $29^\circ$  per unit change in the damping coefficient.

Writing

$$\frac{\partial \bar{P}}{\partial \mu} = \frac{\partial \bar{P}}{\partial \Psi} \frac{\partial \Psi}{\partial \mu} \quad 5.06$$

and combining the evaluations in 5.02, 5.05,

$$\frac{\partial \bar{P}}{\partial \mu} = 34 \times 10^6 \text{ kw.}; \quad 5.07$$

that is, the net power transmitted into the bay must increase with increasing  $\mu$  at the rate of 34 million kilowatts per unit change in  $\mu$ .

Redfield's (1950) equation 5 may be written

$$\frac{(\xi'_0)^2}{2\xi_0^2} = (\cosh 2\mu x + \cos 2kx)^{-1} \quad 5.08$$

where  $\xi'_0$  is the amplitude of tidal oscillation at the reflecting barrier at the head of the bay. Differentiating with respect to  $\mu$ , holding  $\xi_0$  constant,

$$\frac{\partial \xi'_0}{\partial \mu} = \frac{-2\xi_0^2}{\xi'_0} \frac{x \sinh 2\mu x}{(\cosh 2\mu x + \cos 2kx)^2}. \quad 5.09$$

$\xi_0$  will be constant with changing  $\mu$  only at the nodal line. There the tidal range will be that of the wave driving the system (9 feet according to Redfield), and  $kx = -90^\circ$ , so that 5.09 is entered with

$\mu = 1$ ,  $kx = -90^\circ$ ,  $x = -0.25$ ,  $\xi_0 = 4.5$  feet,  $\xi'_0 = 17$  feet, giving

$$\frac{\partial \xi'_0}{\partial \mu} = -14.4 \text{ feet.} \quad 5.10$$

That is, the amplitude of tidal oscillations at the head of the bay will change with change in  $\mu$ , decreasing at the rate of 14.4 feet per unit increase in  $\mu$ .

Writing

$$\frac{\partial \xi'_0}{\partial \bar{P}} = \frac{\partial \xi'_0}{\partial \mu} \frac{\partial \mu}{\partial \bar{P}} = \frac{\partial \xi'_0}{\partial \mu} \frac{1}{\frac{\partial \bar{P}}{\partial \mu}}, \quad 5.11$$

5.07 and 5.10 may be combined to give

$$\begin{aligned} \frac{\partial \xi'_0}{\partial \bar{P}} &= \frac{-14.4}{34 \times 10^6} = -4.2 \times 10^{-7} \text{ foot per kilowatt} \\ &= -0.42 \text{ foot per million kilowatts.} \end{aligned} \quad 5.12$$

That is, the extraction of additional power from the Bay of Fundy system will decrease the tidal amplitude at the head of the bay at the rate of 0.42 foot per million kilowatts.

## 6. IMPLICATIONS FOR TIDAL POWER PROJECTS

Any consideration of extracting usable power from the tides must take cognizance of the power currently involved in the system. Where an appreciable change in the total power of the system is contemplated the effect on tidal ranges must be considered.

The contemplated Passamaquoddy Power Project would close off Passamaquoddy Bay and let it flood at the top of the tidal cycle (high water) and drain

near the bottom (low water). It is contemplated that a  $3 \times 10^6$  kw. installation could be accommodated. If a 50% efficiency is assumed in the generating mechanism a transport of energy at the mean rate of  $6 \times 10^6$  kw. into the bay is required. This would be  $7 \times 10^6$  kw. less than is at present transmitted into the bay.

According to 5.12 one might expect an increase in mean tidal amplitude at the head of the bay given by

$$\Delta \xi'_0 = -0.42 \times -0.7 = 0.3 \text{ foot} \quad 6.01$$

or an increase in mean range 0.6 foot.

This increase would be for the vicinity of Hopewell Cape where the present mean range is 34 feet, and where Redfield's analysis locates the reflecting barrier. At Burntcoat Head, in Manas Basin, the mean range might be expected to increase by 0.7 foot. These changes are roughly equal to the changes Hachey (1934) predicted on the basis of complete closing of Passamaquoddy Bay.

In considering tidal power projects for the head of the Bay of Fundy, it will be necessary to keep in mind not only that the effective damping coefficient will be altered but that the location and efficiency of the reflecting barrier may be altered so as to significantly change the properties of the tidal oscillations.

#### ACKNOWLEDGMENTS

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## Proteins in Fish Muscle. II. On the Extraction of Myosin from Cod Muscle with Potassium Iodide<sup>1,2</sup>

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### ABSTRACT

An attempt has been made to extract myosin from cod muscle using potassium iodide solution as extractant. The product resembled in several respects myosins made from other cold-blooded animals by other methods, and like them, differed from rabbit myosin in solubility and sedimentation behaviour. Comparison was also made with cod actomyosin with respect to electrophoresis, sedimentation, viscosity, and solubility.

DYER (1951) has shown that the quality deterioration that occurs during frozen storage of lean fishes such as cod can be correlated with the loss of solubility of the actomyosin proteins in salt solutions. Since it has not been possible to study the behaviour of these proteins in the muscle itself, a general investigation of their nature after extraction has been undertaken at this laboratory. Myosin, either free or combined, is presumed to be one of the components of these extracts, and the isolation and study of this and the other components is desirable.

Most of the work on myosin and the actomyosin system has been done on extracts of fresh rabbit skeletal muscle, and was recently reviewed by A. G. Szent-Györgyi (1955). The techniques developed for the isolation of myosin have been applied successfully to heart muscle of sheep, calf, cow, and pig by Gelotte (1951), but have so far failed for skeletal muscle of cold-blooded animals like frog and fish. Nevertheless, the existence of an electrophoretic gradient presumed to represent myosin has been demonstrated in extracts of the skeletal muscles of turtles (Dubuisson, 1953), lobsters (Dubuisson-Brouha, 1953), carp (Hamoir, 1949; 1951), and frog (Godeaux, 1952). By ultracentrifugation of a carp actomyosin extract in the presence of adenosine triphosphate (ATP), Hamoir (1951) demonstrated the existence of a substance with a sedimentation constant corresponding to that of rabbit myosin. By using an extracting solution containing ATP, Hamoir and Reuter (1956) have recently succeeded in preparing from frog skeletal muscle a protein that had many of the properties to be expected by analogy with rabbit myosin, but which appeared to be much more labile. Connell (1954) has also reported the preparation from cod muscle, by a modified method, of a protein that may possibly have been myosin.

A. G. Szent-Györgyi (1951a) described the preparation of rabbit myosin both from muscle and from precipitated actomyosin, using a potassium iodide extracting solution. This was based on his observation (1951b) that actin was irreversibly depolymerized by KI in the absence of ATP. The product was completely free of actin, and "behaved in every respect in a manner similar to that of myosin

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obtained by standard methods". This present paper reports the measurements of some of the properties of the protein extracted from cod with this reagent, and comparison is made with those of similar extracts made with KCl, which are generally considered to contain actomyosin.

#### MATERIALS

Fillets cut from cod (*Gadus callarias*) were used in the preparation of the protein extracts. The fish were of various sizes, and were usually filleted within 2 hours of catching, while still in the pre-rigor state. Portions of fillets not used for immediate extractions were stored in polyethylene bags at 1°C. Extractions could thus be made on portions of the same fillet both before and after it had passed through rigor mortis. Using samples cut from the middle of the fillet and weighing 25 g., the water-extractable proteins ("albumins") were first removed by two successive extractions in a two-speed Waring blender, using each time 450 ml. of a cold dilute potassium phosphate buffer ( $\Gamma/2 = 0.05$ , pH = 6.6)<sup>3</sup>, and recovering the residue by centrifuging at 1,500×g. Blending time was 5 seconds at high speed followed by 55 seconds at low speed in each case. For all extractions, the blender was fitted with a baffle under the liquid surface to prevent vortex formation (Dyer *et al.*, 1950), and operated under slight air pressure to prevent entrance of air through the bearing. The residue from the second extraction was blended for 60 seconds ("high speed" at 90 volts) with 400 ml. of a cold solution containing either 0.6 M KCl or 0.6 M KI, together with potassium phosphate buffer to give a total ionic concentration of  $\Gamma/2 = 0.8$ , pH = 7.4. Such solutions are hereafter called "KCl-phosphate", etc. The extracts were centrifuged at 1,500×g, and unless otherwise stated, those made with KI were dialyzed in cellulose tubing (Visking) against three changes of KCl-phosphate of  $\Gamma/2 = 0.8$ , pH = 7.4 (10 volumes), in order to replace the iodide, and to permit comparison to be made with the KCl-extracts. During blending, the temperature of the solution rose to between 5 and 10°C.; centrifuging, dialysis, and other preparative procedures were carried out in a cold room at 1°C. Usually more than 80% of the total muscle protein could be accounted for in the extracts. KI tended to give slightly more complete extraction than KCl, and extraction of post-rigor fillets was more complete than that of pre-rigor fillets.

Protein was determined by the biuret procedure of Snow (1950). Chloride concentration was either calculated from known dilutions, or determined by the method of Dyer (1943).

#### RESULTS

##### ELECTROPHORESIS

Electrophoresis was carried out in a Klett Tiselius-type free boundary apparatus using a KCl-phosphate buffer of  $\Gamma/2 = 0.40$ , and pH as indicated, at a tem-

<sup>3</sup>The symbol  $\Gamma/2$  is used in this paper to denote "ionic concentration", defined as  $\sum_i \frac{C_i z_i^2}{2}$

where  $C_i$  is the concentration of the  $i^{\text{th}}$  ion species expressed as moles per litre. At low concentrations,  $\Gamma/2$  is approximately equal to  $\mu$ , the ionic strength.

perature of 0.8°C. It was found that if lower ionic concentrations were used, there was a tendency to form sharp, false boundaries, presumably due to aggregation of the protein molecules as the threshold of precipitation was approached. At higher ionic concentrations, the higher currents necessary led to excessive heating effects. Because of the strong turbidity of the KCl-extracts, it was difficult to observe the entire boundary in the electrophoresis cell, unless the protein concentration was not greater than 0.3 mg. N/ml.

A typical pattern of a KCl-extract made after prior extraction of the albumins is shown in Fig. 1. The very sharp leading edge of the peak on the ascending side and the more symmetrical descending peak are characteristic of actomyosin. No other peaks could be detected. This extract was made from a medium-sized cod (approximately 18 inches long) just entering rigor, but post-rigor specimens gave entirely similar patterns. The solvent for electrophoresis in this case was KCl-phosphate of  $\Gamma/2 = 0.40$ , pH = 7.4 and the ascending mobility was  $-3.30 \times 10^{-5} \text{ cm}^2 \text{ v}^{-1} \text{ sec}^{-1}$ . In a preliminary preparation run in NaCl-phosphate of  $\Gamma/2 = 0.30$ , pH = 7.2, the ascending mobility was  $-2.77 \times 10^{-5} \text{ cm}^2 \text{ v}^{-1} \text{ sec}^{-1}$ , in close agreement with the value of  $-2.78 \times 10^{-5} \text{ cm}^2 \text{ v}^{-1} \text{ sec}^{-1}$  for carp myosin- $\beta$  in NaCl-phosphate at  $\mu = 0.35$ , pH = 7.1 (Hamoir, 1951). Presumably, the difference in mobilities in potassium and sodium buffer solutions was due in part to a difference in the binding of  $\text{K}^+$  and  $\text{Na}^+$  ions.

Figure 2 shows the electrophoretic pattern obtained for a KI-extract of the same cod used to obtain that of Fig. 1. The solution was much less viscous and less cloudy than the corresponding KCl-extract. The main peak (2) had a slightly higher mobility than the actomyosin of Fig. 1, and the ascending side was more symmetrical. The area of the minor peak (1) measured by planimeter from an enlarged tracing, and subject to a considerable error because of doubt in the positioning of the base line, varied between 11.5 and 16.0% of the total area in various extracts of this type. Similar patterns were obtained for KI-extracts of pre-rigor and post-rigor cod. Runs were also made at pH values down to 6.5. The patterns remained unchanged, while the mobilities of both peaks decreased somewhat. Unfortunately, it was not possible to locate the iso-electric point because the protein became insoluble at about pH 6.0 and ionic concentration 0.40.

If the protein obtained by a KCl-extraction was precipitated by dilution to  $\Gamma/2 = 0.1$ , redissolved in 0.3 M, 0.6 M, or 1.0 M KI, and the KI replaced with KCl by dialysis, the electrophoretic patterns of the resulting solutions were again similar to those just described. If, however, solutions of protein that had been extracted with, or treated with KI were diluted to  $\Gamma/2 = 0.1$ , and the precipitated protein redissolved in KCl, the patterns showed only one peak with the same mobility as the main peak of the KI-extracts. There was, however, an increased dissimilarity in shape between the ascending and descending patterns (Fig. 3). Usually, not all of the precipitated protein would redissolve in  $\Gamma/2 = 0.8$  KCl-phosphate solution (pH = 7.3); the amount remaining insoluble depended upon the time of precipitation, and upon the time and field of centrifuging. The electrophoretic pattern of the protein remaining soluble at

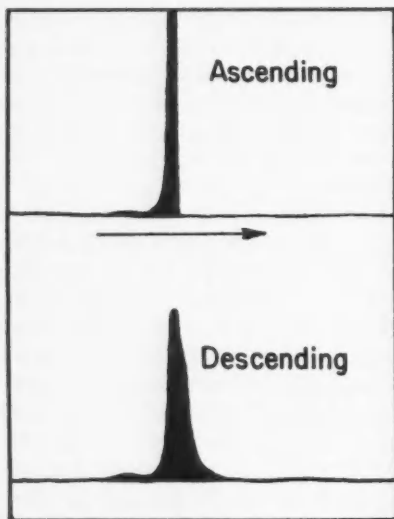


FIG. 1

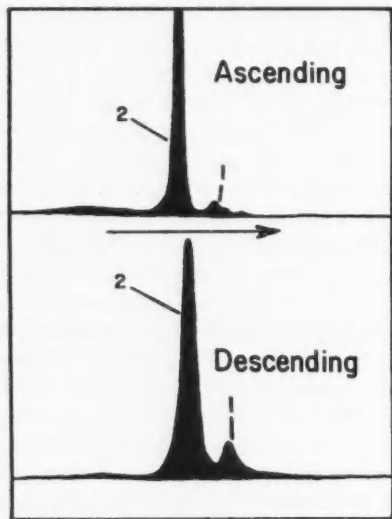


FIG. 2

FIG. 1. Electrophoretic pattern of a KCl-extract of cod in rigor.

$\Gamma/2 = 0.4$ , pH = 7.46. Field strength, 2.30 v./cm. Duration of electrophoresis, 400 min. Protein concentration, 0.258 mg. N/ml. Migration from left to right. Mobilities ( $\times 10^5$  cm.<sup>2</sup>v.<sup>-1</sup>sec.<sup>-1</sup>): ascending, -3.30; descending, -3.13.

FIG. 2. Electrophoretic pattern of a KI-extract of cod in rigor.

$\Gamma/2 = 0.4$ , pH = 7.38. Field strength, 2.26 v./cm. Duration of electrophoresis, 375 min. Protein concentration, 0.776 mg. N/ml. Migration from left to right. Mobilities ( $\times 10^5$  cm.<sup>2</sup>v.<sup>-1</sup>sec.<sup>-1</sup>): ascending—peak 1, -4.58; peak 2, -3.50; descending—peak 1, -4.58; peak 2, -3.34.

$\Gamma/2 = 0.1$  indicated the presence of one major and two minor components (Fig. 4). The mobility of the major peak (2) agreed with that of the more rapid component in the unfractionated extract (peak 1, Fig. 2).

The electrophoresis results indicate that KI caused a dissociation of actomyosin into at least two components, which may be myosin (the major component) and actin, as claimed by A. G. Szent-Györgyi (1951a). The mobilities were somewhat higher, however, than those reported by Connell (1954) for his preparations of cod myosin and actin in similar solvents. Most evidence so far reported suggests that a similar dissociation of actomyosin is brought about by the addition of ATP (see, for example, Weber, 1956), and it would be useful to compare the pattern of actomyosin in the presence of ATP with that of a KI-extract. Unfortunately, this did not prove possible, because when 0.7 g./l. of ATP was added to a KCl-extract, together with versene to inhibit the ATP-ase action of the protein by removal of  $\text{Ca}^{++}$  and  $\text{Mg}^{++}$ , practically all of the protein was precipitated at  $\Gamma/2 = 0.4$  and pH = 7.4.

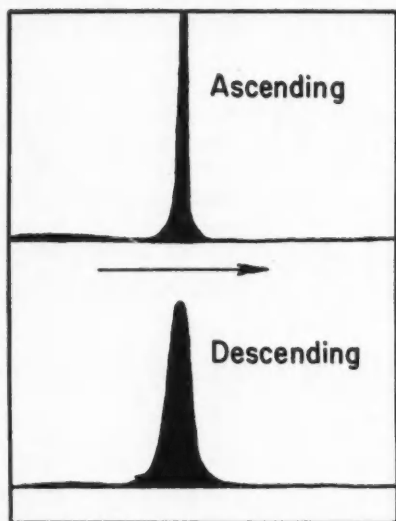


FIG. 3

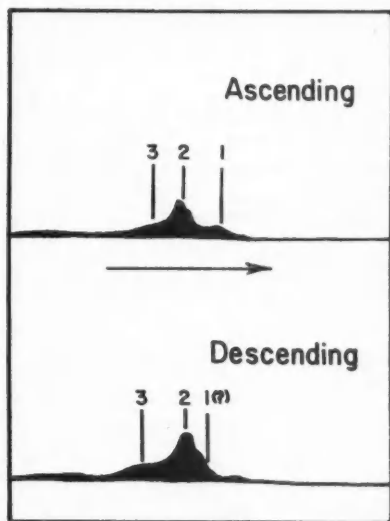


FIG. 4

FIG. 3. Electrophoretic pattern of a KI-extract of cod in rigor, after precipitation by dilution and re-solution in KCl-phosphate.

$\Gamma/2 = 0.4$ , pH = 7.23. Field strength, 2.28 v./cm. Duration of electrophoresis, 361 min. Protein concentration, 0.387 mg. N/ml. Migration from left to right. Mobilities ( $\times 10^6$  cm.<sup>2</sup>v.<sup>-1</sup>sec.<sup>-1</sup>): ascending -3.41; descending, -3.31.

FIG. 4. Electrophoretic pattern of the water-soluble fraction of a KI-extract of cod in rigor.  $\Gamma/2 = 0.4$ , pH = 7.42. Field strength, 2.24 v./cm. Duration of electrophoresis, 250 min. Protein concentration, 0.156 mg. N/ml. Migration from left to right. Mobilities ( $\times 10^6$  cm.<sup>2</sup>v.<sup>-1</sup>sec.<sup>-1</sup>): ascending—peak 1, -5.9; peak 2, -4.64; peak 3, -3.3; descending—peak 1, -6.4(?); peak 2, -4.76; peak 3, -3.30.

#### SEDIMENTATION

Sedimentation runs were made in a Spinco Model E ultracentrifuge at 59,780 r.p.m. The temperature of the rotor was usually about 20°C., but occasionally rose to 25°C. The sedimentation constants are given in Svedberg units for the conditions of the run, and are not corrected to water at 20°C.

The sedimentation pattern of a typical KCl-extract of a post-rigor cod is shown in Fig. 5(A). The patterns of KCl-extracts of pre-rigor cod were similar except in the proportions of the four peaks. In a separate investigation at this laboratory, it was found that the two components represented by peaks 1 and 2 were labile, especially at higher temperatures. The size of the peaks diminished during storage of the fillets and there was a corresponding increase in the size of the two slower-sedimenting peaks, 3 and 4, and in the amount of the gel that was rapidly sedimented even at lower speeds. The sedimentation constants of peaks 1 and 2 depended upon protein concentration while those of peaks 3 and 4 were steady at approximately 6.0 and 2.5 respectively. Peaks 1 and 2 are suspected to be actomyosins, while 3 is probably myosin (Ellis, in preparation).

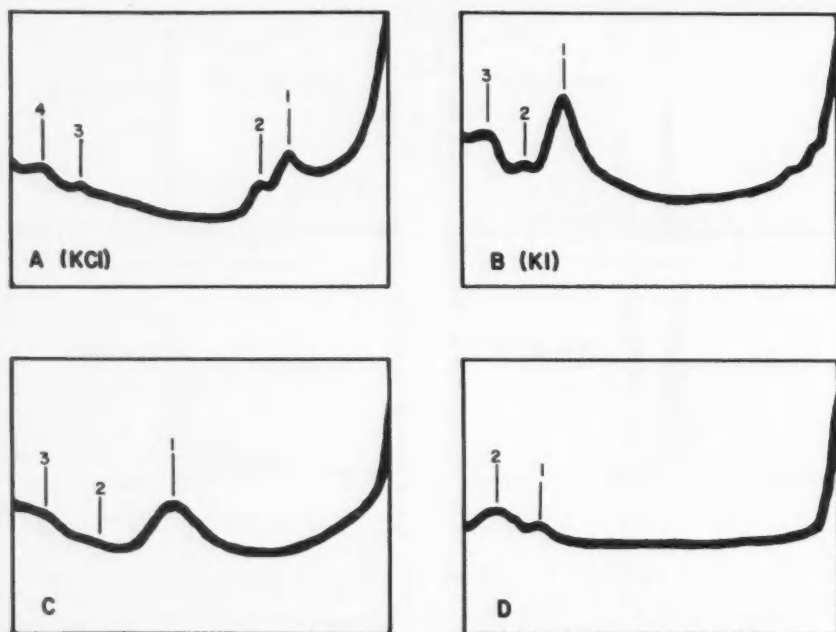


FIG. 5. Sedimentation patterns of extracts of post-rigor cod muscle.

Speed of centrifuging, 59,780 r.p.m. Migration from left to right. Solvent, KCl-phosphate pH = 7.4. Temperature approx. 20°C.

Curve A: KCl-extract in KCl-phosphate.

Curve B: KI-extract after dialysis against KCl-phosphate.

Curve C: water-insoluble fraction of KI-extract, precipitated and redissolved in KCl-phosphate.

Curve D: water-soluble fraction of KI-extract.

Curve	Ionic concentration	Protein	Time of centrifuging	Sedimentation constants			
				1	2	3	4
		mg. N/ml.	min.		Svedberg units		
A	0.80	~0.85	24	23.5	21.3	5.5	2.7
B	0.80	0.881	24	9.3	6.4	2.5	...
C	0.80	0.717	20	13.5	—	—	...
D	0.16	0.432	34	6.1	2.6	...	...

A typical pattern of a KI-extract, after replacement of KI with KCl by dialysis, is shown in Fig. 5(B). Instead of the two rapid peaks of the KCl-extract, there was a well-defined peak with sedimentation constant  $s'$  of about 9 to 17, depending upon protein concentration, pH, ionic concentration, and age of extract. There were also two minor peaks, 2 and 3, which were unaffected by ionic concentration and pH, and apparently identical with peaks 3 and 4 of the KCl-extract. The protein precipitated by dilution of the KI-extract, when redissolved in KCl-phosphate solution, gave a similar pattern, although the main peak was less well defined, and the minor peaks were very weak (Fig.

5(C)). The corresponding water-soluble fraction apparently consisted of the two minor components with  $s' = 6.1$  and  $2.6$  respectively at  $\Gamma/2 = 0.16$  and  $\text{pH} = 7.4$  (Fig. 5(D)).

An example of the effects of ionic concentration and  $\text{pH}$  on the sedimentation constants of the components of a pre-rigor KI-extract is given in Table I. In this case peak 2 (Fig. 5(B)) could not be observed. Protein concentration was  $0.60$  to  $0.67$  mg. N/ml. except at  $\Gamma/2 = 0.4$  and  $\text{pH} = 6.4$ , when it was  $0.43$  mg. N/ml. The extracts had been stored for 5 to 7 days at  $1^\circ\text{C}$ . It can be seen that while the sedimentation constant of peak 3 remained almost unaffected, that of the major peak (1) varied inversely with both ionic concentration and  $\text{pH}$ .

TABLE I. Effect of  $\text{pH}$  and ionic concentration on the sedimentation constants of the components of a KI-extract of pre-rigor cod.

$\Gamma/2$	Peak number (see Fig. 5(B))	$s'$ in Svedberg units		
		$\text{pH} = 7.4$	$\text{pH} = 7.0$	$\text{pH} = 6.4$
0.8	1	11.9	11.4	...
	3	2.4	2.5	...
0.4	1	13.3	14.7	17.3
	3	2.5	2.6	2.9

The sedimentation constants of the slower peaks were unaffected by protein concentration. Data relative to the effect of this variable on the constant of the major peak (peak 1 of Fig. 5(B)) are summarized in Fig. 6. The difference between the curves for the pre-rigor and post-rigor KI-extracts was probably not significant because points determined for analogous extracts of other cod samples did not consistently fall on one curve or the other. The differences can probably be ascribed to variations in extract ages, and to accidental changes in temperature during storage and handling. Data reported for frog myosin (Hamoir and Reuter, 1956), carp myosin (Hamoir, 1951) and cod myosin (Connell, 1954) are included for comparison. It should be noted that the data for the present work refer to KI-extracts that have not been precipitated. In other experiments where the protein was precipitated and redissolved, the sedimentation constant became larger and the peak more diffuse (Fig. 5(C)) in agreement with the findings of Hamoir and Reuter (1956), who thought that this behaviour indicated aggregation of the myosin particles.

The effect of the addition of ATP to a KCl-extract of cod is shown in Fig. 7(C). The very prominent and well-defined peak 2 had a sedimentation constant between  $5.4$  and  $6.0$  in various preparations, and is similar to that which has been considered (e.g. Hamoir, 1951) to be myosin in similarly treated extracts from other animals. The curve given by that author for the sedimentation constant of the analogous peak in carp extracts is shown in Fig. 6, and it agrees with the values found in the present work. It was also thought desirable to examine the sedimentation pattern of the KCl-extract at high ionic concentration since it



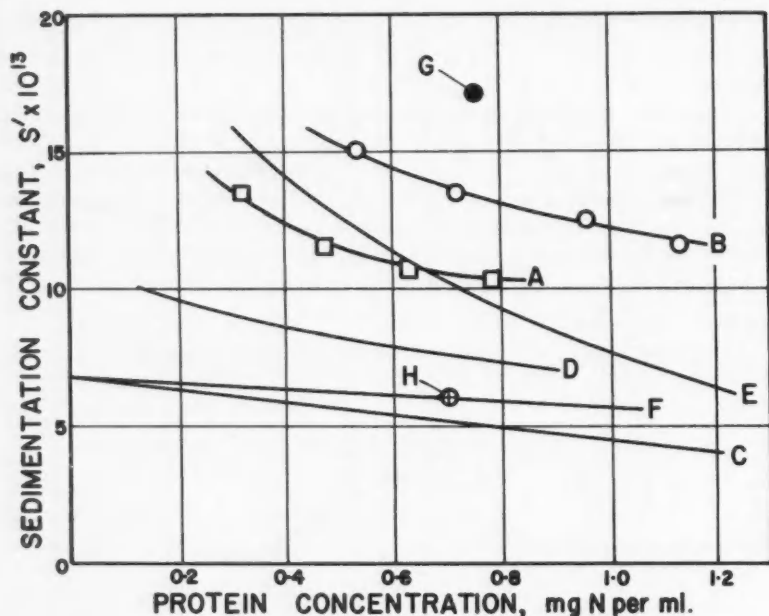


Fig. 6. Dependence of sedimentation constants of "myosin" upon protein concentration. Solvent for curves A and B, and point H, KCl-phosphate,  $\Gamma/2 = 0.8$ , pH = 7.4. Curve A: KI-extract of pre-rigor cod. Curve B: KI-extract of post-rigor cod. Curve C: frog actomyosin plus ATP (Hamoir and Reuter, 1956). Curve D: frog myosin, unprecipitated (Hamoir and Reuter, 1956). Curve E: frog myosin, "purified by precipitation" (Hamoir and Reuter, 1956). Curve F: carp actomyosin plus ATP (Hamoir, 1951). Point G: cod "myosin" (Connell, 1954). Point H: KCl-extract of post-rigor cod, plus ATP.

was claimed by Guba (1943), A. Szent-Györgyi (1949) and Johnson and Landolt (1951) that actomyosin was dissociated into actin and myosin under these conditions. Portzehl *et al.* (1950), on the other hand, thought that this claim was dubious. Figure 7(B) shows the pattern obtained when a KCl-extract was ultracentrifuged at an ionic concentration of 2.0, obtained by dissolving solid KCl in the regular extract at  $\Gamma/2 = 0.80$  and pH = 7.4. The peaks became very broadened, some material of  $s' = 69$  was observed, and only a very small peak of  $s' = 5.3$  that might correspond to myosin was apparent. When, however, ATP was added at  $\Gamma/2 = 2.0$ , the same characteristic peak as before was observed, although it was somewhat slower ( $s' = 4.2$ ; Fig. 7(D)). It was also noted that in the preliminary centrifuging at  $31,000\times g$  before the ultracentrifuge run the sample with ATP at  $\Gamma/2 = 2.0$  gave a smaller residue than that without ATP. Thus it appears that although high ionic concentration may cause some dissociation of actomyosin, the effect is certainly not as profound as that caused by ATP. Bárány *et al.* (1951) have also reported that the two effects are different.



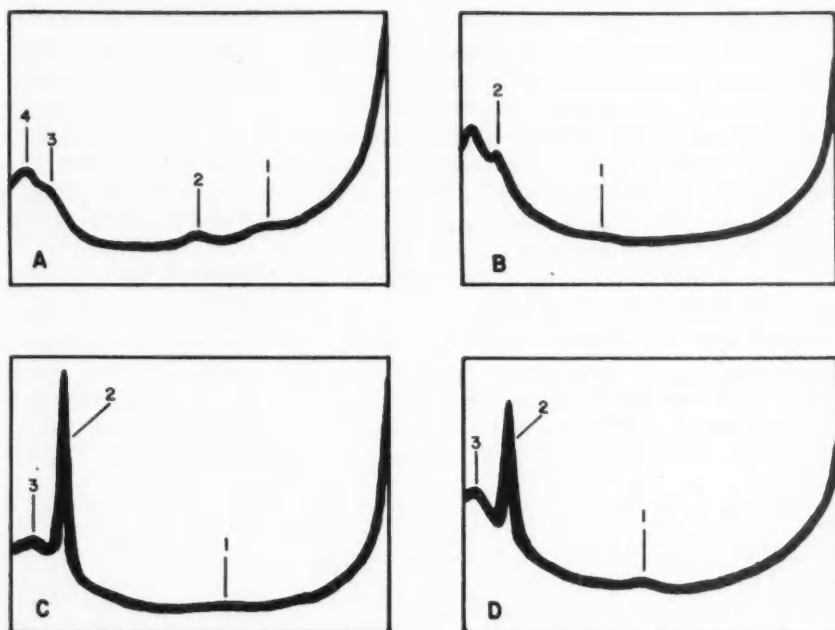


FIG. 7. Effect of ionic concentration and ATP on the sedimentation pattern of KCl-extract of post-rigor cod.

Speed of centrifuging 59,780 r.p.m. Migration from left to right. Solvent, KCl-phosphate,  $r/2 = 0.2$ , pH = 7.4, plus KCl. Temperature 20 to 25°C.

Curve	Ionic concentration	Protein	ATP	Time of centrifuging	Sedimentation constants			
					1	2	3	4
		mg. N/ml.	g./l.	min.	Svedberg units			
A	0.80	0.70	0	16	41.6	29.4	5.7	2.4
B	2.0	0.69	0	16	34.2	5.3	...	...
C	0.80	0.72	0.7	24	22.0	5.6	2.5	...
D	2.0	0.69	0.7	24	17.9	4.8	1.7	...

The effects of KI and of ATP on the sedimentation pattern of cod actomyosin (KCl-extracts) therefore appeared to be qualitatively similar, but the analogy was spoiled by the difference in the size and concentration-dependence of the sedimentation constant of the main component in the two cases. The same difference in behaviour between the ATP-produced component and isolated myosin was also noted by Hamoir and Reuter (1956) for frog, and can be deduced from Connell's work (1954) with cod myosin, although in the case of rabbit there was good agreement (see for example, Portzehl *et al.*, 1950). The difference may be associated with the marked lability and tendency to aggregate that has been noted for myosin of cold-blooded animals. The nature of the minor peaks in the patterns of the KI-extracts is not known, but presumably they should represent tropomyosin and possibly inactive G-actin.

# VISCOSITY

Viscosity measurements were made at 0.3°C. in modified Ubbelohde capillary viscometers constructed with horizontal U-shaped capillaries. This enabled a suitable length of relatively large-bore capillary to be used (approximately 1.6 mm. diameter, 55 cm. long) which would minimize errors due to any surface denaturation of the protein that might occur. In some measurements, flow rate was increased by applying controlled pressures, but conditions were not attained in which the flow was Newtonian. Because of the varying velocity gradients, the reported viscosity values are merely indicative.

Representative curves of specific viscosity,  $\eta_{sp} = \frac{\eta_{\text{solution}}}{\eta_{\text{solvent}}} - 1$ , as a function of protein concentration for both types of extract are shown in Fig. 8. In this case, pre-rigor cod muscle was extracted, but viscosity curves for extracts from post-rigor muscle of the same sample of cod were usually indistinguishable. If the KCl-extract was allowed to age, its viscosity was found to decrease, while that of the KI-extract (in KCl) was found to increase with time to a lesser extent. On several occasions, the KI-extract set to a gel after about 2 weeks at 1°C.

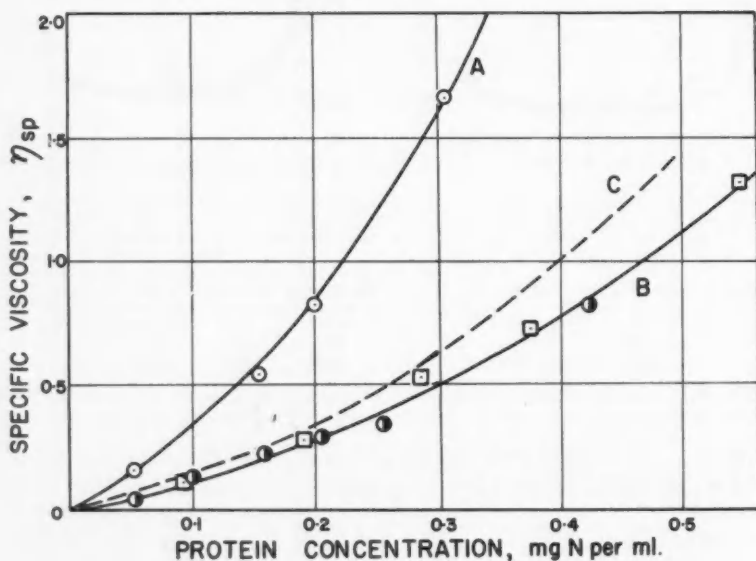


FIG. 8. Dependence of specific viscosity on protein concentration for KCl- and KI-extracts of pre-rigor cod.

Solvent, KCl-phosphate,  $\Gamma/2 = 0.80$ , pH = 7.4. Temperature 0.3°C.

Curve A: KCl-extract (actomyosin).

Curve B: KI-extract (after dialysis against KCl-phosphate).

Curve C: same as B, corrected for content of 15% of water-soluble protein of low viscosity.

Points 1: KCl-extract plus ATP (0.7 g. ATP/l. + 0.002 M  $\text{MgSO}_4$ ).

Points are also shown in Fig. 8 for mixtures of the KCl-extract and ATP. The amount of ATP used was found in a separate experiment to give maximum change in viscosity. It was remarkable that these points fell close to the curve for the KI-extract. It should be noted that the KI-extract had not been fractionated, and therefore all the data presented in Fig. 8 should be directly comparable. The addition of ATP to the KI-extract was found to be entirely without effect on the viscosity; this is one of the principal characteristics of myosin, differentiating it from actomyosin.

The intrinsic viscosities indicated by the above data can be seen in Fig. 9.

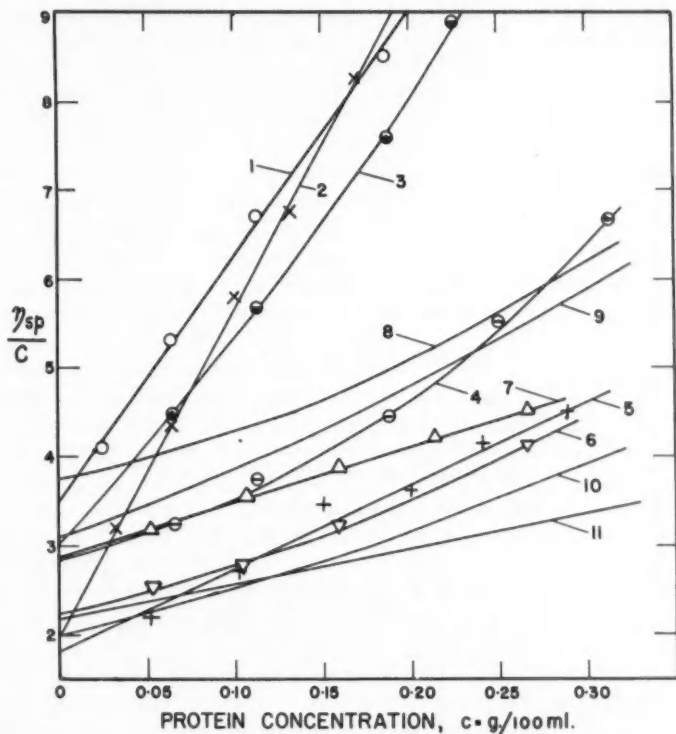


FIG. 9. Intrinsic viscosities of various protein preparations.

Solvent (for curves 1 to 7), KCl-phosphate,  $\Gamma/2 = 0.8$ , pH = 7.4. Temperature 0.3°C.

Curves 1, 2, and 3: KCl-extracts of post-rigor cod, 2 to 3 days after extraction.

Curve 4: KCl-extract of post-rigor cod, 9 days after extraction.

Curves 5 and 6: KI-extracts of post-rigor cod, 3 to 4 days after extraction.

Curve 7: KI-extract of post-rigor cod, 9 days after extraction.

Curve 8: rabbit actomyosin (Mommaerts, 1945).

Curve 9: cod actomyosin (Connell, 1954).

Curve 10: cod "myosin" (Connell, 1954).

Curve 11: frog myosin (Hamoir and Reuter, 1956).

In order to compare the present results with those of others, the viscosities of the KI-extracts were corrected for the water-soluble proteins they contained. These amounted to approximately 15% of the total protein, and their contribution to the viscosity was found to be very small after removal of the myosin-like protein by dialysis to a low ionic concentration. In general, the viscosities of the KCl-extracts, presumably actomyosin, tended to be very high, and only approached those of Mommaerts' (1945) rabbit actomyosin and Connell's cod actomyosin after aging for about one week. The curves for the KI-extracts, on the other hand, agreed at least roughly with those reported for myosins by others. The causes of the lack of reproducibility in the viscosity data, especially for the KCl-extracts, are not known, but they could perhaps be associated with minor variations in procedure, or with the condition of the fish before extraction.

The variation of the viscosities of the extracts with ionic concentration was also investigated and the results were plotted in Fig. 10. The ionic concentrations

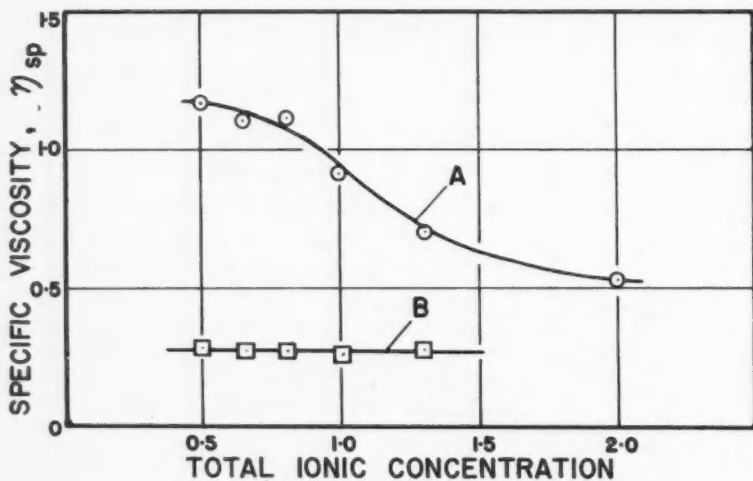


FIG. 10. Variation of specific viscosity of a KCl-extract of pre-rigor cod as a function of ionic concentration.

Solvent, KCl-phosphate, pH = 7.4, molarity of KCl = total ionic concentration  $\times 0.75$ . Temperature, 0.3°C.

Curve A: extract without ATP added. Protein concentration, 0.218 to 0.194 mg. N/ml.

Curve B: same extract after addition of 0.7 g. ATP/l. and 0.002 M  $\text{MgSO}_4$ . Protein concentration, 0.218 to 0.224 mg. N/ml.

were varied by adding water or concentrated KCl-phosphate solution (pH = 7.4) to aliquots of the regular extracts at  $\Gamma/2 = 0.8$ , pH = 7.4, and a solution of ATP and  $\text{MgSO}_4$  was added when required to give a final concentration of 0.7 g./l. ATP and 0.002 M  $\text{MgSO}_4$  (constant total volume). At the higher ionic

concentrations, the amount of protein removed in the preliminary centrifuging of the KCl-extract at 16,000 r.p.m. was somewhat increased, so that the protein concentration of the sample at  $\Gamma/2 = 2.0$  was approximately 10% below that at  $\Gamma/2 = 0.8$ . No correction was made for this. In the samples containing ATP, however, the loss upon centrifuging was small. While the viscosity of the KCl-extract decreased with increasing ionic concentration, the curve appeared to level out at a value higher than that for the samples containing ATP. The viscosity of the latter was unaffected by ionic concentration. It was also found that the viscosity of the KI-extract was independent of ionic concentration between  $\Gamma/2 = 0.8$  and 2.2, showing further resemblance to ATP-treated actomyosin.

These viscosity data as well as the sedimentation data indicate that the blending technique used in extracting the cod actomyosin did not seriously affect the characteristic sensitivity of this protein toward ATP, and so the blending would appear not to be the cause of the lack of ATP-sensitivity in the KI-extracts. The similarity of the viscosity behaviour of the KI-extracts to that of ATP-treated actomyosin and the fair agreement with the viscosities reported for other preparations of myosins strongly indicate, although not conclusively, that KI caused a permanent dissociation of actomyosin into actin and myosin. The viscosity data also add further support to the assertion that ATP and high ionic concentration do not have the same effect on actomyosin.

#### SOLUBILITIES

In determining the solubility as a function of the ionic concentration, aliquots of the extracts in KCl-phosphate solution ( $\Gamma/2 = 0.80$ , KCl = 0.6 M, pH as indicated) were diluted by addition to suitable precooled mixtures of the same solution and water to give samples of various ionic concentrations at constant volume and constant total protein content. After standing for about 17 hours at 1°C., they were centrifuged at 31,000 $\times$ g in plastic tubes, and the soluble protein was determined in the supernates. In order to make it possible to compare the results for various extracts, they were expressed as percentage of the total protein in the aliquots that was soluble in an identically treated mixture at  $\Gamma/2 = 0.80$ . At this ionic concentration there was only a trace of residue after centrifuging, and the concentration in the supernate was usually in the range 0.10 to 0.12 mg. N/ml. The reproducibility of the curves for analogous extracts from various samples of fish was in general very good, and the curves reported are representative.

The solubilities of protein of a given type of extract were identical whether made from pre-rigor or post-rigor muscle, but the KCl-extracts and KI-extracts differed from each other characteristically as shown in Fig. 11. This Figure also shows the solubility of the KI-extract when KI-phosphate was the solvent, before replacement of this with KCl by dialysis. When measured in the same solvent, the protein of the KI-extract remained soluble to distinctly lower ionic concentrations than the KCl-extract. The solubility of the fresh KCl-extract fell off more abruptly, while that of the KI-extract fell off more gradually, especially at the lower limit of solubility.

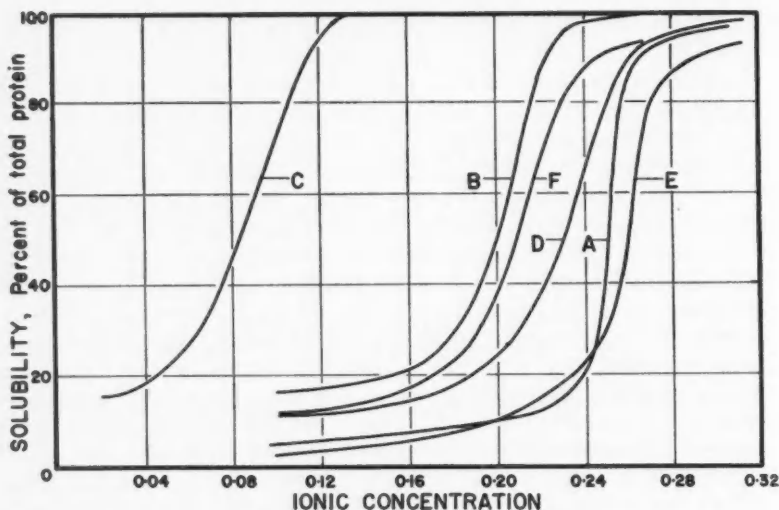


Fig. 11. Solubility of proteins extracted from post-rigor cod.

Solvent (except Curve C), KCl-phosphate, pH = 7.4, molarity of KCl = ionic concentration  $\times 0.75$ . Temperature, 1°C.

Curve A: KCl-extract, stored 1 day.

Curve B: KI-extract, stored 2 days.

Curve C: KI-extract in KI-phosphate as solvent.

Curve D: KCl-extract, stored 15 days.

Curve E: KCl-extract, precipitated by dilution and redissolved in KCl-phosphate.

Curve F: KCl-extract, precipitated by dilution, redissolved in KI-phosphate, and dialyzed against KCl-phosphate.

Another noteworthy feature was the "residual" solubility in the two cases. With the KCl-extract, approximately 5% remained soluble at low ionic concentrations while the corresponding value for the KI-extract was usually about 15%. These values were found to hold even at ionic concentrations as low as 0.0035, attained by dialysis of the respective extracts. In one experiment, for example, the concentration of KI in the extracting solutions was varied from 0 to 1.2 M, while each contained potassium phosphate buffer at  $\Gamma/2 = 0.20$  and pH = 7.4. The albumins had been largely removed by three preliminary extractions at  $\Gamma/2 = 0.05$ . The limiting solubilities at a final ionic concentration of about 0.01 after dialysis are given in Table II. In several experiments, in which the electrophoretic pattern was determined at the same time, it was found that residual solubility of the KI-extracts corresponded approximately with the percentage area of the rapid peak in the electrophoretic patterns.

The changes upon aging of the KCl-extract, already noted for sedimentation and viscosity, were reflected in its solubility as shown in Fig. 11 (Curves A and D). After 15 days the protein had become more soluble at lower ionic concentrations, suggesting a dissociation into smaller particles. The KI-extract showed no significant change up to 9 days, but probably would exhibit decreased solu-

TABLE II. Residual solubilities of protein in various extracts of post-rigor cod after dialysis to  $\Gamma/2 = 0.01$ .

Extract number	Extracting solution		Limiting solubility, total protein
	$\Gamma/2$ (KCl)	$\Gamma/2$ (KI)	
1	0.6	0.0	5.8
2	0.3	0.3	12.5
3	0.0	0.6	14.0
4	0.0	1.2	15.6

bility after a longer interval since such extracts were occasionally found to have set to a gel after about 2 weeks.

The solubility of actomyosin after precipitation by dilution of a KCl-extract and dissolution in either KCl-phosphate or KI-phosphate at  $\Gamma/2 = 0.8$ , pH = 7.4 (the latter followed by dialysis against KCl-phosphate) is also shown in Fig. 11 (Curves E and F, respectively). The more gradual slope and the shift to higher ionic concentrations of the solubility curve of the protein redissolved in KCl suggested an increase in heterogeneity. The curve for the protein dissolved in KI, on the other hand, was practically parallel to that of a direct KI-extract. The displacement downwards could be accounted for by the partial elimination of the water-soluble portion of the actomyosin extract as a result of the precipitation.

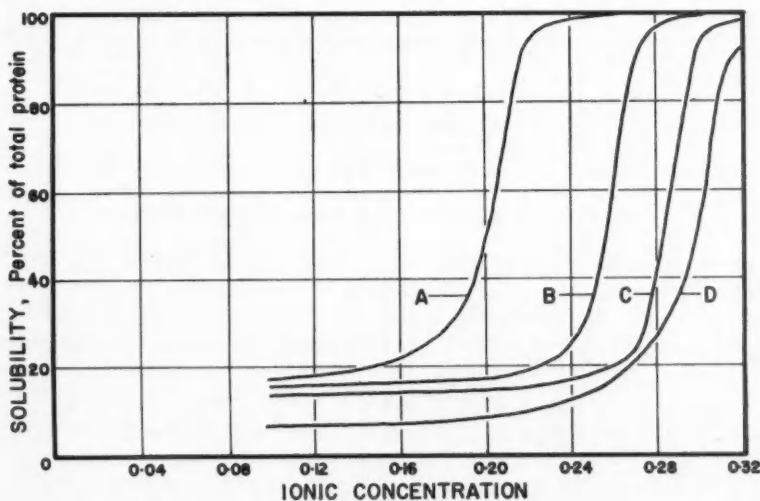


FIG. 12. Effect of pH on solubility of protein extracted from pre-rigor cod. Solvent, KCl-phosphate. Temperature, 1°C. Extracts had been stored for 4 to 6 days at 1°C.

Curve A: KI-extract at pH 7.4.

Curve B: KI-extract at pH 7.0.

Curve C: KI-extract at pH 6.6.

Curve D: KCl-extract at pH 6.6.

The effect of pH on solubility of the KI-extract is shown in Fig. 12. At pH 6.6 the curve approached that for the KCl-extract under the same conditions (except for the limiting solubility at low  $\Gamma/2$ ). Further data on the dependence of solubility on pH at several fixed ionic concentrations are given in Fig. 13. In this case, a KI-extract had been precipitated by dilution and redissolved in 0.5 M NaCl brought to pH 7.5 with  $\text{NaHCO}_3$ , thus eliminating most of the water-soluble fractions.

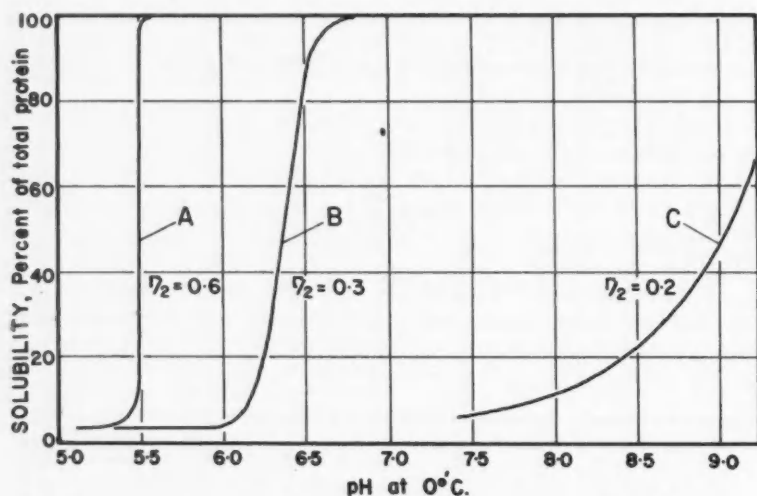


FIG. 13. Solubility of KI-extract of post-rigor cod as a function of pH.

Temperature, 1°C. Solvents:

Curve A: 0.55 M NaCl+Na phosphate buffers, total  $\Gamma/2 = 0.60$ .

Curve B: 0.25 M NaCl+Na phosphate buffers, total  $\Gamma/2 = 0.30$ .

Curve C: 0.15 M NaCl+Na borate buffers, total  $\Gamma/2 = 0.20$ .

Attempts were made to fractionate the KI-extract by dilution to various ionic concentrations followed by redissolving the centrifuged precipitate at  $\Gamma/2 = 0.8$ , pH = 7.4. It was usually found that the first precipitates formed could not be completely redissolved, and that the solutions of the most soluble fractions were nearly clear. No further work was attempted on the least soluble fraction, since the change in solubility indicated that it had been modified even by the comparatively mild process of isolation. It was unlikely that it was actomyosin, however, since the original solubility curve did not overlap to any great extent that of the KCl-extract. The solubility of the more soluble fractions as a function of the total amount of protein in the system was determined. The less soluble protein was first removed by dialysis to  $\Gamma/2 = 0.21$  at pH = 7.4. Samples of the remaining supernate were then added to suitable mixtures of KCl-phosphate solution and water to give a series of samples of increasing total protein content at constant volume and  $\Gamma/2 = 0.18$ , pH = 7.4. The curve showing the concentration of protein remaining soluble is given in Fig. 14. Correction was made



for the portion of the protein in the samples that remained soluble at very low ionic strength, so that the data refer only to the salt-soluble protein. The precision of the measurements was not sufficient for a decision whether the solubility should be represented by a straight line, or by a curved one passing through the origin. The latter should be the case if the solid phase was a solid solution of two or more proteins of differing solubilities. In either case, the protein was clearly heterogeneous, probably with respect to particle size.

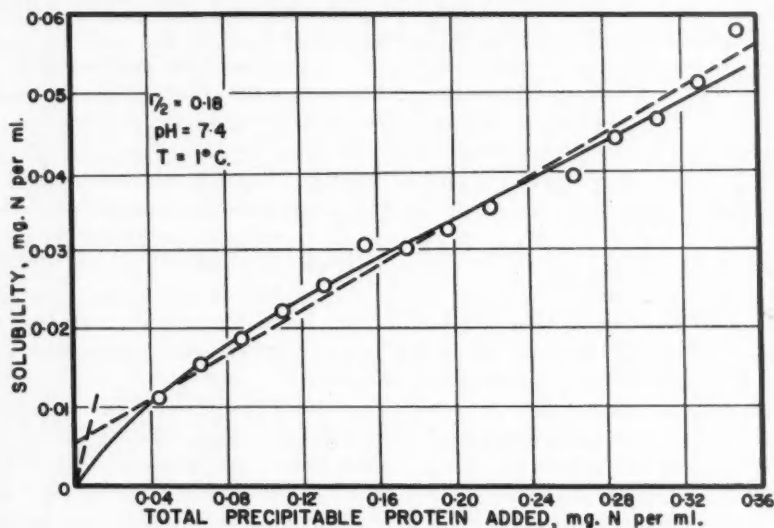


FIG. 14. Solubility curve of KI-extract of post-rigor cod (fraction soluble below  $\Gamma/2 = 0.21$ , pH = 7.4).

Solvent, KCl-phosphate,  $\Gamma/2 = 0.18$ , pH = 7.4.

The solubility results indicate that KI causes a dissociation of actomyosin into at least two components. The water-soluble one, amounting to approximately 10% of the salt-extractable protein of the muscle, could be actin. If so, this would indicate that cod actomyosin is much poorer in actin than is rabbit actomyosin, which is generally considered to contain from 25 to 33% actin. It is possible that the 5% residual solubility in the KCl-extracts represents tropomyosin. The solubility of the water-insoluble fraction of the KI-extracts appears to agree with the solubility of frog myosin (Hamoir and Reuter, 1956), and also approximately with that of rabbit myosin according to the scanty data given by Portzehl *et al.* (1950). A. Szent-Györgyi (1947, p. 135), however, claimed that rabbit myosin was soluble even in 0.1 M KCl, and also at  $\mu = 0.001$ , but insoluble at intermediate values. Present data did not seem to indicate that cod "myosin" was soluble at very low ionic concentrations. The data of Portzehl *et al.* (1950) also show that rabbit actomyosin was precipitated at somewhat higher ionic concentrations (0.30 to 0.34 at pH 6 to 7) than has been found for cod actomyosin.

## DISCUSSION

The resemblance of the sedimentation and of the viscosity behaviour of cod actomyosin in the presence of ATP to that of rabbit actomyosin under similar conditions strongly suggests that a cod myosin should exist. It may be expecting too much to suppose that cod myosin should be nearly identical with rabbit myosin in all its properties, but it should at least possess the ability to interact with actin, be itself insensitive to the addition of ATP, and be able to dephosphorylate this substance. A general similarity to rabbit myosin with respect to solubility and viscosity should also be expected.

We have not yet been able to determine the ability of the protein extracted from cod with KI to combine with actin, and its ATP-ase properties have not been studied, but it does appear to have some of the other properties to be expected for myosin. The viscosity was completely unaffected by the addition of ATP, and by increase in ionic concentration. The electrophoretic properties were in fair agreement with those of myosins prepared from muscle of other animals. The protein precipitated at lower ionic concentrations than did actomyosin, and a larger proportion of the total protein remained soluble at very low ionic concentration, indicating that a dissociation of actomyosin had been effected by KI. The sedimentation behaviour, while not agreeing with that of rabbit myosin, did resemble that of frog and of Connell's cod myosin, and was decidedly different from that of cod actomyosin.

It is most unlikely that the proteins extracted by KI could be considered homogeneous, and this may account for the sedimentation behaviour. The KI-extracts were very opalescent, and the turbidity could not be removed by centrifuging at  $31,000\times g$ . Moreover, it tended to increase upon standing. Hamoir (1956) has stated, on the other hand, that solutions of frog myosin were water-clear, and remained so even when some aggregation had apparently occurred. He also suggested that in the present case some denaturation may have taken place. This could certainly be so on account of the tendency to form minute bubbles by cavitation during blending. There was also the possibility of contamination from heavy-metal ions. Ordinary distilled water was used since it seemed pointless to use glass-distilled water as recommended by various authors, if the solutions were to be exposed to various metals during blending and other operations. The cod "myosin" also seemed to be rather labile, apparently becoming aggregated when precipitated or when the extracts were allowed to age, similar to the behaviour described by Hamoir (1956) for frog myosin and by Portzehl *et al.* (1950) for rabbit myosin.

It seems possible, therefore, that extraction of cod muscle with KI solutions results in a dissociation of actomyosin, and that myosin can be recovered in a somewhat altered form from such an extract. A definite claim for this cannot be made, however, until the interaction of the protein with actin and ATP have been studied.

## ACKNOWLEDGMENTS

The author is indebted to W. J. Dyer and D. G. Ellis for helpful suggestions during the course of this work, and to the latter and J. T. Lauder for carrying out the ultracentrifuge runs.

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# Physical Oceanographic Results of the "Calanus" Expeditions in Ungava Bay, Frobisher Bay, Cumberland Sound, Hudson Strait and Northern Hudson Bay, 1949-1955<sup>1</sup>

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"CALANUS" SERIES No. 15

## ABSTRACT

Results of the physical oceanographic work of the "Calanus" expeditions of 1949-55 are presented in summary. Bathymetric maps are given for Ungava Bay, Frobisher Bay and north-east Hudson Bay. Temperature, salinity and density profiles are used to show the direction of flow of water, without dynamic calculations. Temperature-salinity correlation diagrams show the presence of Atlantic water below 100 metres, well developed in Cumberland Sound, less so in Ungava Bay and Hudson Strait (but still present), and very slight in northern Hudson Bay. In Frobisher Bay the entry of Atlantic water, if it occurs, is masked by tidal turbulence. Inversions of density, giving temporary negative stabilities, are recorded at a number of stations, concentrated in the regions of large tidal ranges; association of these inversions with the state of the tide is indicated. Stability conditions of the water in general are presented; the winter régime in northern Hudson Bay offers no reason to doubt that a normal vertical exchange of water occurs. Special hydrographic conditions in certain inlets are described. The dominance of the whole hydrodynamic pattern by the tides, especially in the eastern part of the area under study, is emphasized.

## INTRODUCTION

THE "CALANUS" EXPEDITIONS of 1947 and 1948, the first two years of operations, were not concerned to any significant degree with physical oceanography. Such material as was obtained has already been published (Dunbar, 1951). The expeditions of 1949 and 1950 worked within the limits of Ungava Bay with the exception of a few days spent in the Button Islands in the eastern end of Hudson Strait in both years, and a section (Section V) across Hudson Strait from Wakeham Bay to Big Island made in 1950. During the winters of 1948-49, 1949-50 and 1950-51 the ship was beached in Frenchman's Cove at Fort Chimo, on the Koksoak River. In the 1951 season one section (Section VI) was made from the mouth of the Korok River to Akpatok Island, and the remainder of the season's work was done in southeast Baffin Island, principally in Frobisher Bay. The *Calanus* was beached at Frobisher Bay airfield for the 1951-52 winter. The 1952 season was cut short owing to engine trouble, and the hydrographic results were restricted to a few stations in Cumberland Sound. The ship was drawn up on the marine railway at Churchill for the winters of 1952-53 and 1953-54. The working seasons of 1953 and 1954 were spent in the northern part of Hudson Bay

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and the northwestern end of Hudson Strait. Stations occupied by Mr. A. W. Mansfield in April, May and June, 1955, working through the ice, have also been incorporated into this report.

The hydrographic sections are shown on the accompanying maps (Fig. 1, 2 and 3). For other stations referred to in the present paper, see the station lists already published (Dunbar and Grainger, 1952; Grainger, 1954; Grainger and Dunbar, 1956).

#### METHODS

The *Calanus* is a 43-ton diesel ketch equipped with echo-sounder, trawl gear, dredges, plankton gear and the usual hydrographic equipment. During most of the field work Bergen Nautik reversing water samplers were used, with Negretti and Zambra deep-sea thermometers. Unprotected thermometers were not used,

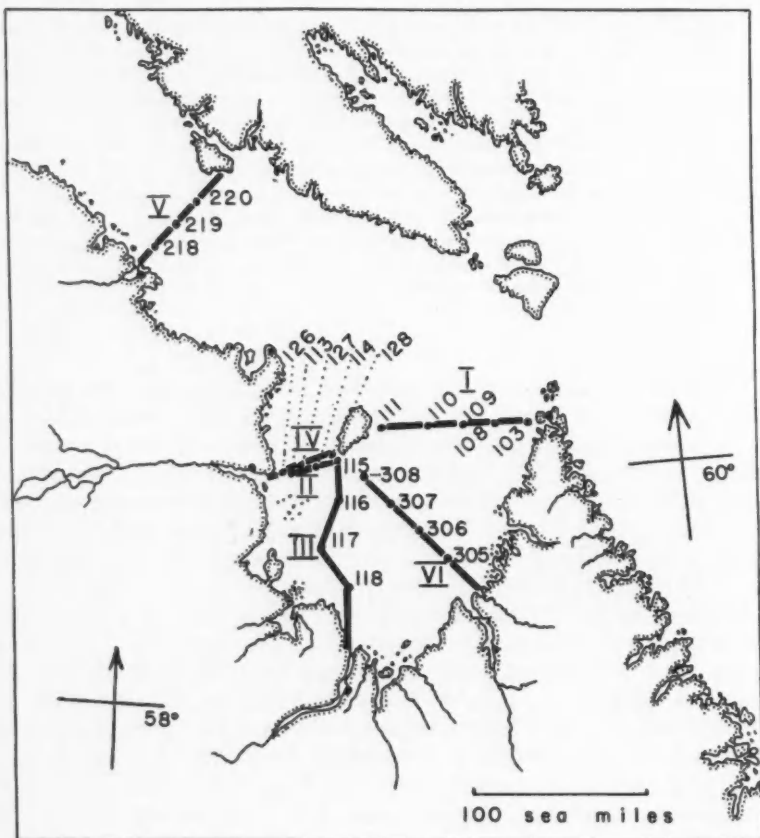


FIG. 1. Hydrographic sections in Ungava Bay and Hudson Strait (Sections I-VI).

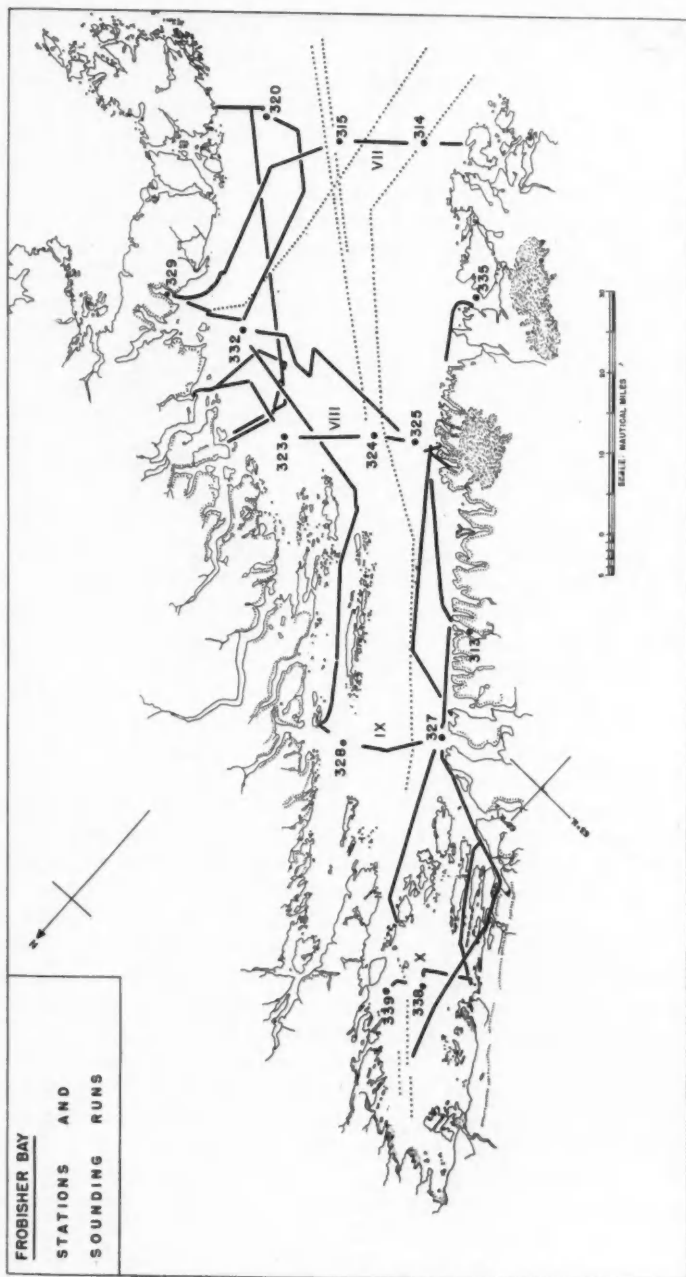


FIG. 2. Sections (VII-X) and hydrographic stations in Frobisher Bay, 1951. Solid lines: sounding runs made by the *Calanus*. Dotted lines: sounding runs taken from U.S. Hydrographic Office Chart No. 5854 (1944), corrected to 1950.

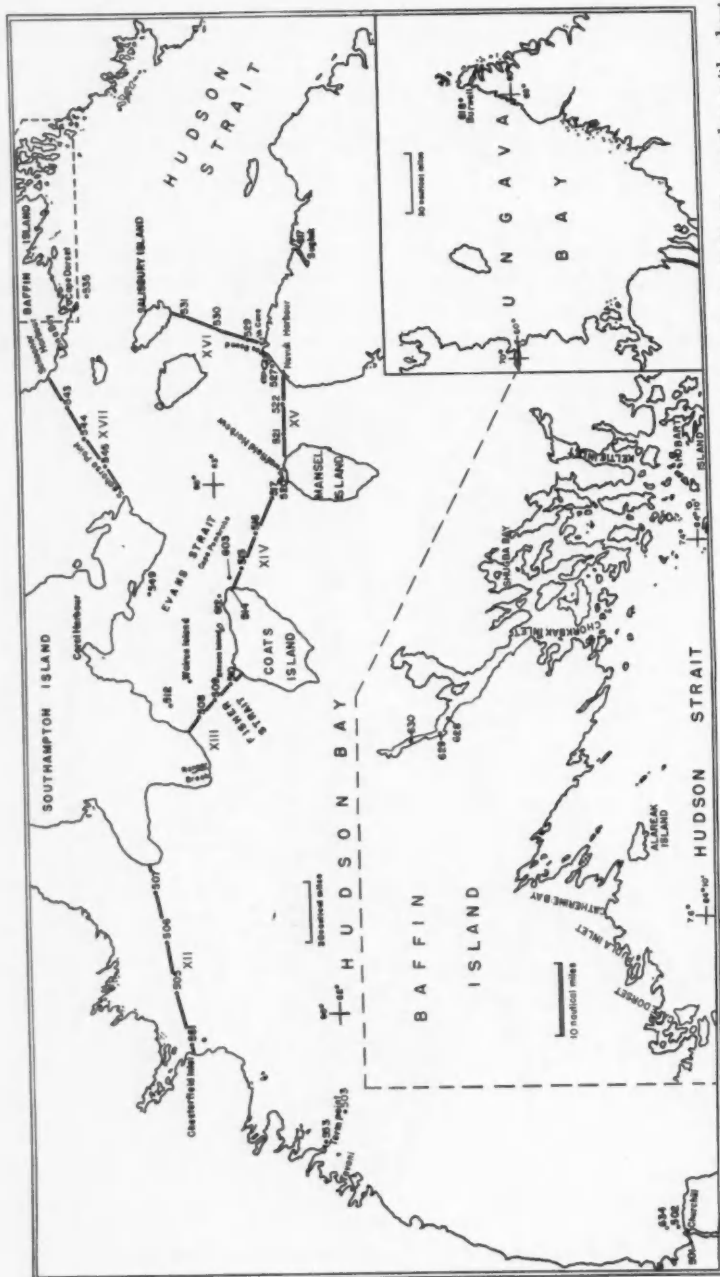


FIG. 3. Hydrographic stations and Sections (XII-XVII) in northern Hudson Bay and western Hudson Strait, 1953-54; together with chart showing position of Station 618 (1954) in Ungava Bay.



and there may consequently be small errors in the depths of observation. These errors, however, were kept down to a minimum by making hydrographic observations only in fairly calm weather; wire angles were usually normal to the surface and were very seldom less than  $80^\circ$ .

The water samples were preserved in 200–250 ml. glass bottles with bakelite screw tops, up to the end of the 1952 season, after which Danish citrate bottles were used. Both types of bottle are safe against evaporation for the periods of time involved. Titration for chlorinity was done in the Fisheries Research Board of Canada Oceanographic Laboratories at St. Andrews, N.B., through the kindness of Dr. H. B. Hachey. Oxygen and phosphate concentrations were determined in the field, but are not included in the present paper.

Dynamic calculations of horizontal water movement have not been made, for two reasons: (1) the dominant and masking influence of the tides in the areas under study, particularly the eastern part, and (2) the impossibility of finding a motionless horizontal reference level in these shallow and turbulent coastal waters.

#### BATHYMETRY

The general bathymetry of the Canadian eastern Arctic is fairly well known, but detail in certain areas has still to be filled in. The *Calanus* made sounding runs in Ungava Bay, Frobisher Bay, and the region between Foxe Channel, the western end of Hudson Strait, and Coats and Mansel Islands, in all of which the soundings were incomplete. The results of this work, together with soundings published since 1950 by the Canadian Hydrographic Service, are given in Fig. 4, 5 and 6.

The western and southern portions of Ungava Bay are shallow, generally less than 100 m. deep (Fig. 4). There is a channel over 200 m. deep which enters the bay in the northwest and skirts the western and southwestern shores of Akpatok Island. Although soundings are not yet quite extensive enough for certainty, this channel probably continues to the south of Akpatok Island, and certainly runs northward again in the eastern half of the bay. There are depressions in this channel which exceed 300 m. in depth. There is some water over 400 m. deep west of Killinek Island off the extreme northern tip of Labrador, and in fact the 400-m. contour forms the northern boundary of Ungava Bay. Akpatok Island thus forms the highest part of a *massif* which is separated from the mainland by a channel or "moat" of over 200 m. depth, a finding which is in agreement with the remarkable geological difference between the island and the mainland surrounding it.

The bottom of Ungava Bay is irregular, apparently lifted into ridges and heavily loaded with boulders, giving the impression of a terrain recently glaciated, probably with numerous eskers and lateral moraines, and with too short a lapse of time since the retreat of the ice to allow sedimentation to exert any great smoothing effect. It offers, in consequence, almost no good trawling grounds and even makes the use of the dredge somewhat hazardous. The bottom material, apart from rock, is heavy glacial mud with sand.

Frobisher Bay (Fig. 5) contains the deepest water the *Calanus* has so far worked in. The southwestern half of the bay is by far the deeper, containing inside a deep threshold at the mouth of about 300 m. sill depth a trough of over 600 m. maximum depth which lies very close to the steep southwestern shore and extends to the inner group of islands. In the outer part of the bay, outside the outer islands, this deep water gives way fairly steeply towards the northeast, and the bottom finally forms a flat shelf (the Calanus Shelf) which gradually shallows off toward the northeast shoreline. The Calanus Shelf offers excellent trawling bottoms consisting of sandy mud with shells and fine gravel, but the fauna itself is not rich.

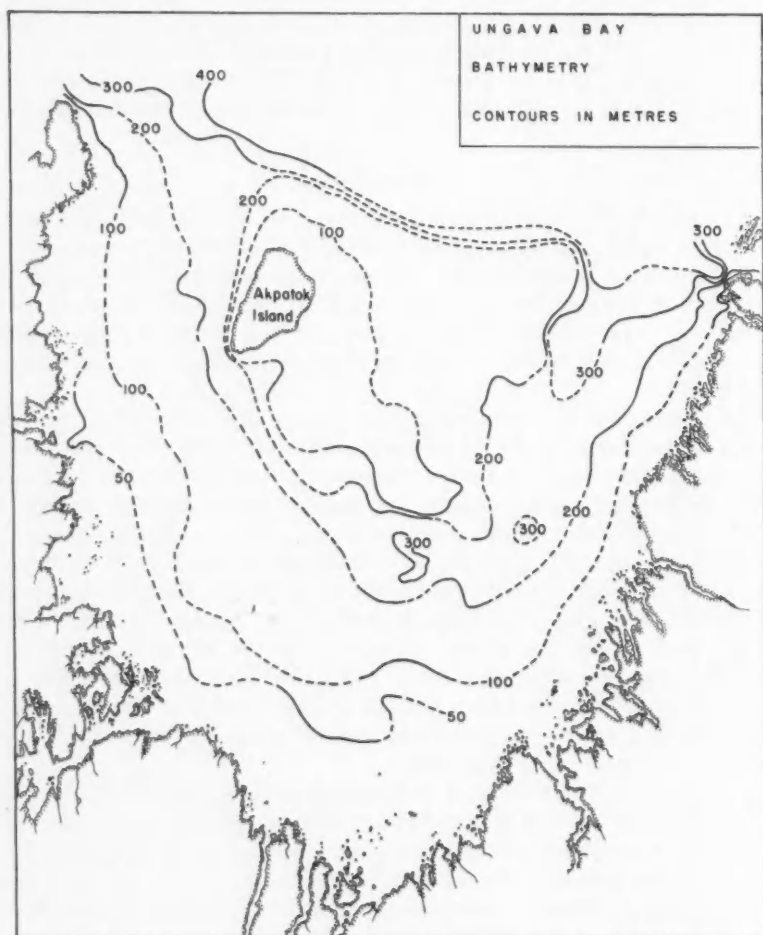


FIG. 4. Bathymetry, Ungava Bay, based on published data and *Calanus* observations.



FIG. 5. Bathymetry, Frobisher Bay.

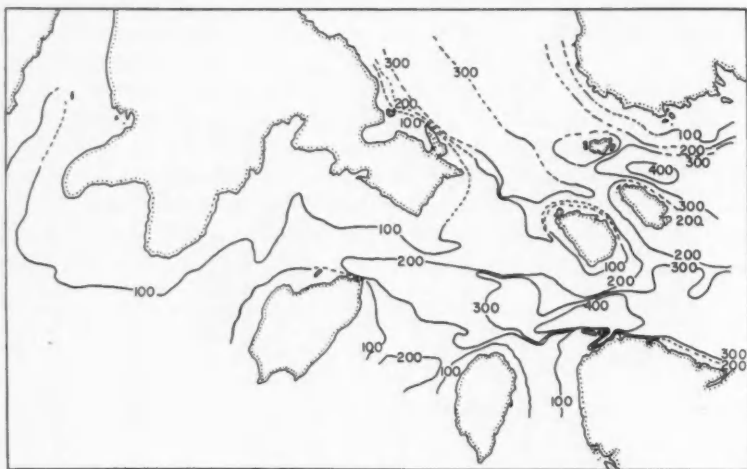


FIG. 6. Bathymetry, northern Hudson Bay and the western entrance to Hudson Strait. Depths in metres.

The outlet from Hudson Bay, between the Coats, Mansel, Salisbury, Mill and Nottingham islands, has been poorly sounded until quite recently, and there has therefore been doubt about the presence or absence, and position, of a possible shallow threshold between Hudson Bay and Hudson Strait. Such a threshold would have had considerable bearing on our understanding of the circulation within Hudson Bay. It now appears, however, as shown in Fig. 6, that there is no threshold between northwestern Quebec and southwestern Baffin Island (Foxe Peninsula), the channels being over 300 m. deep south of Nottingham Island and just under 300 m. north of the island. The shallowest water in the whole area shown in Fig. 6 is between Southampton Island and the mainland of Quebec, across Coats and Mansel Islands, and even here the sill between Coats and Mansel is almost 200 m. deep, or not much less than the deepest water within Hudson Bay. There is therefore very little to hinder free exchange of deep water between Hudson Bay and Hudson Strait.

#### PROFILES OF SECTIONS

##### UNGAVA BAY (Sections I-IV and VI; Fig. 7-11)

In some of these as in certain other sections described in this paper there are instances of density inversions shown by aberrations of the profiles. These are discussed under a subsequent heading.

The Ungava Bay sections were run on the following dates:

Section I, July 16, 1949; Section II, July 21, 1949; Section III, July 21-22, 1949; Section IV, August 23-24, 1949; Section VI, July 24, 1951.

Figures 8 and 10 show a southerly current through Sections II and IV, which

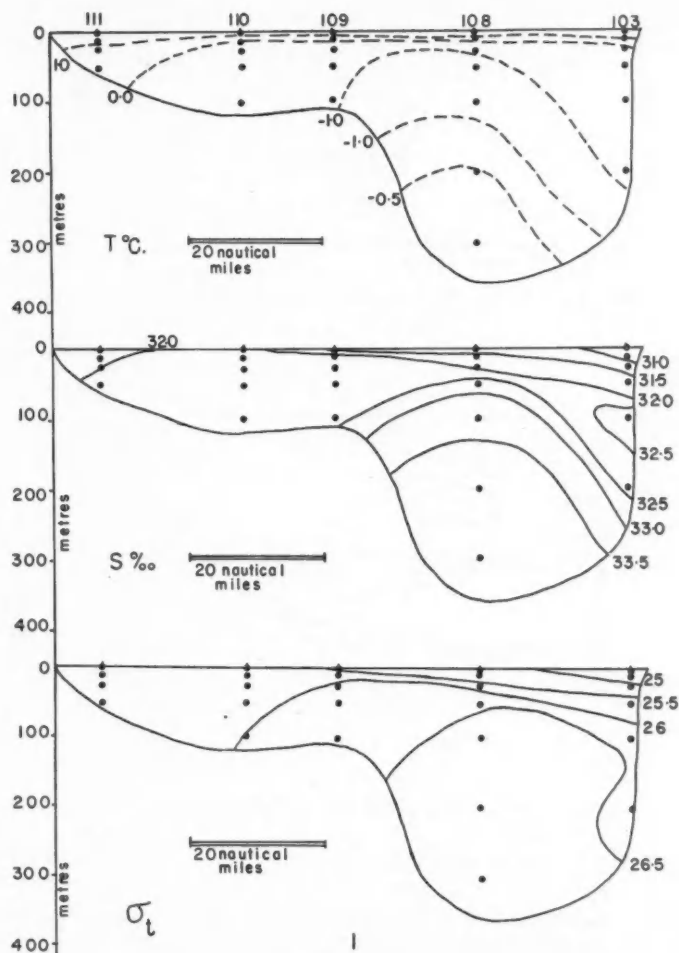
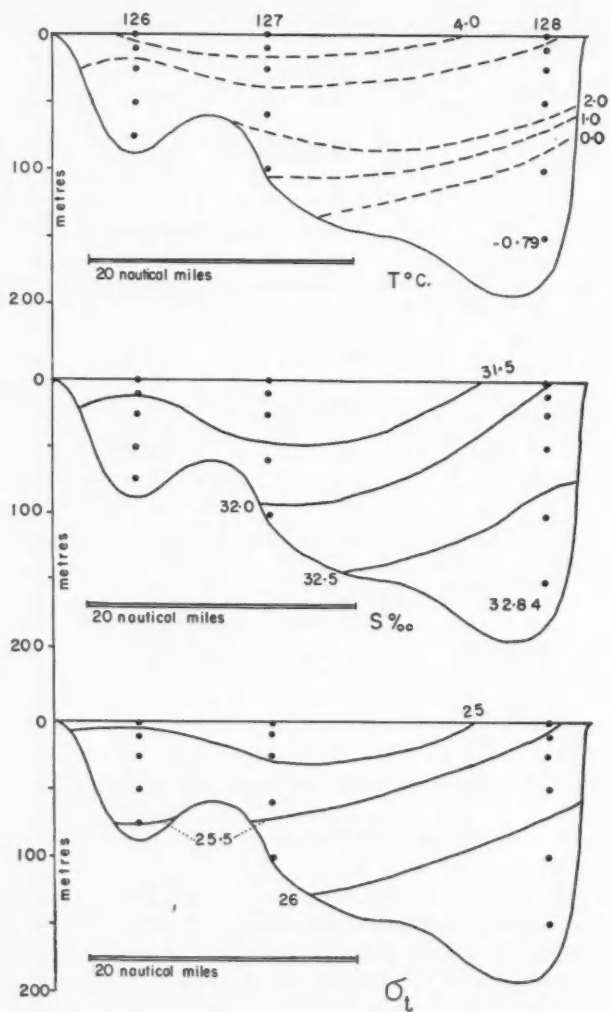


FIG. 7. Temperature, salinity and density profiles, Section I.

lie close together but which were occupied a month apart. The southerly current between Payne River and Akpatok Island is developed differently in the two sections, Section II showing a more strongly developed current in the western part, Section IV in the deeper water against Akpatok Island. Section IV shows a weak northward movement between Stations 126 and 127, possibly an eddy development. Sections III and VI indicate that this southward movement is not continued round the southern tip of Akpatok; instead it flows further to the south and apparently weakens considerably. It can be seen, turned in an eastward direction, between Stations 117 and 116 in Section III, and between Stations



IV

FIG. 10. Temperature, salinity and density profiles, Section IV.

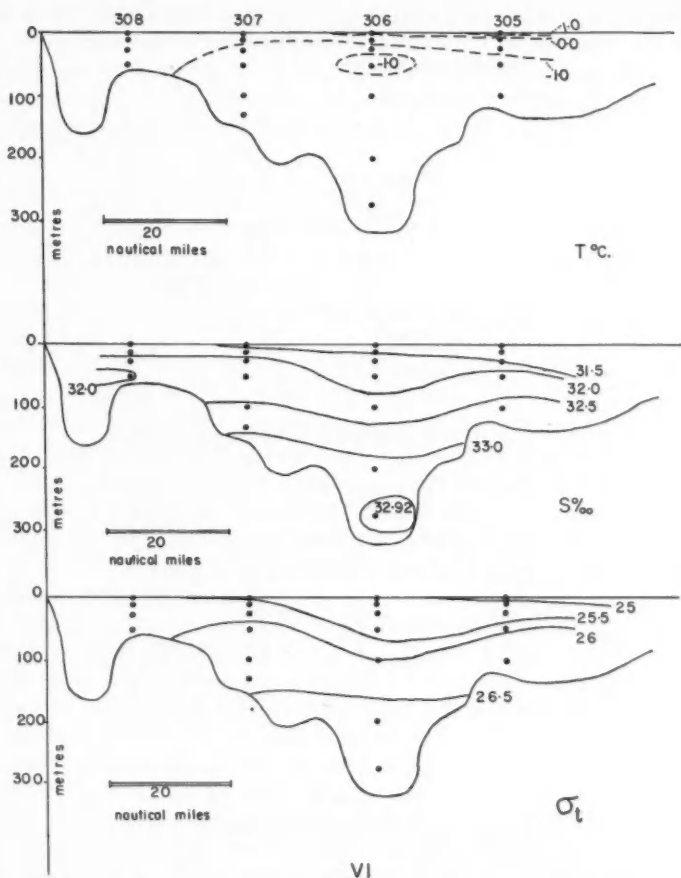


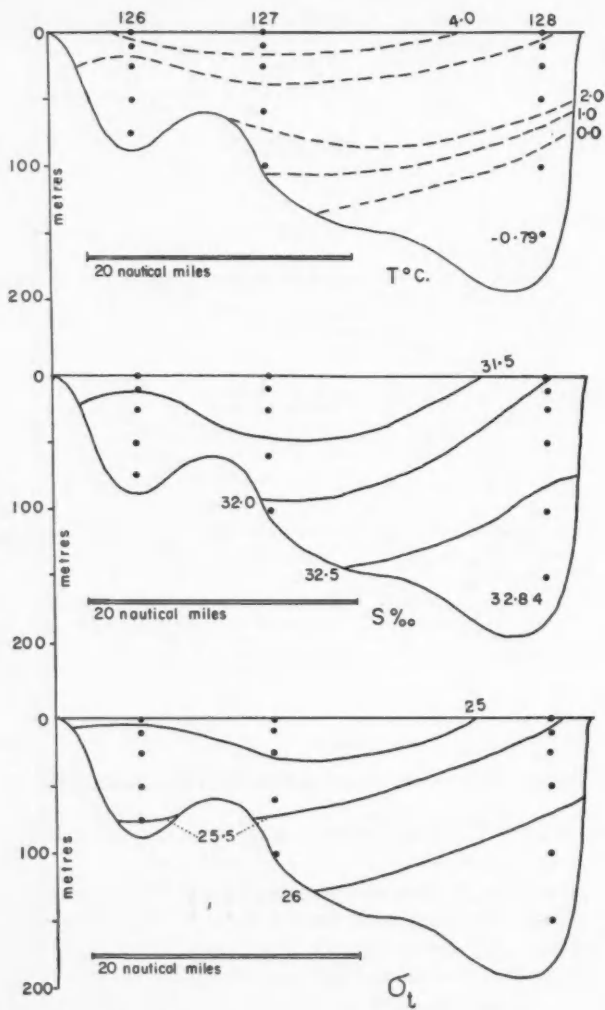
FIG. 11. Temperature, salinity and density profiles, Section VI.

and 109 as a shallow surface current over-riding the southward current deeper down.

The details of the movement of these currents are not shown by the present material. Sections III and VI indicate a complicated play and counterplay of water, with the development of eddies, a situation which is to be expected in a region of such fierce tidal intervention. The possible correlation of undulant profiles, such as are shown in Sections III and VI, with tidal action, has been discussed by Bailey (1955), quoting Riis-Carstensen (1936) and Küllerich (1939).

#### HUDSON STRAIT (Section V, Fig. 12)

Section V, across Hudson Strait from Wakeham Bay to Big Island, is straightforward except for the density inversions in deep water, and shows the already



IV

FIG. 10. Temperature, salinity and density profiles, Section IV.



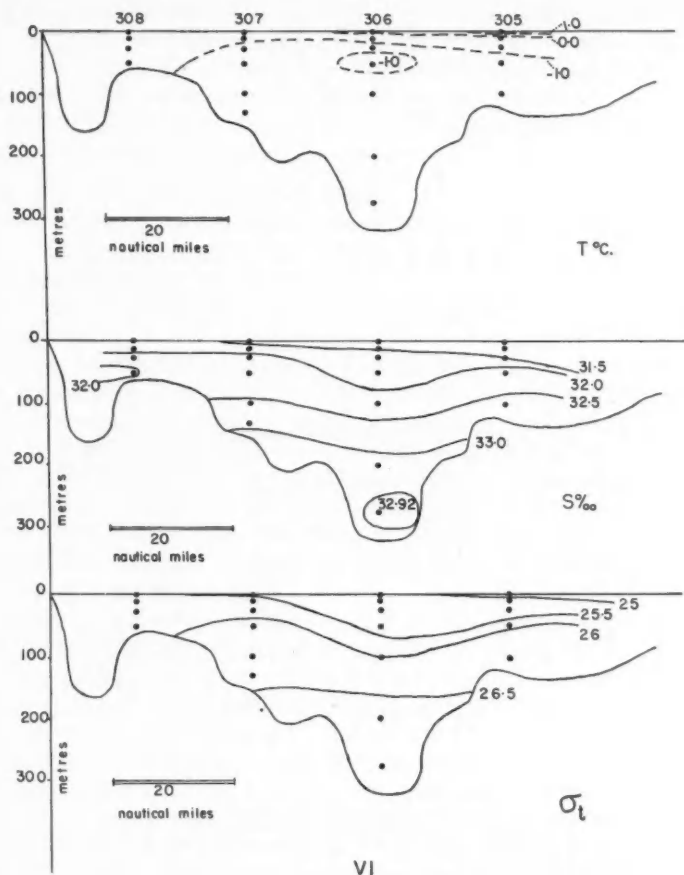


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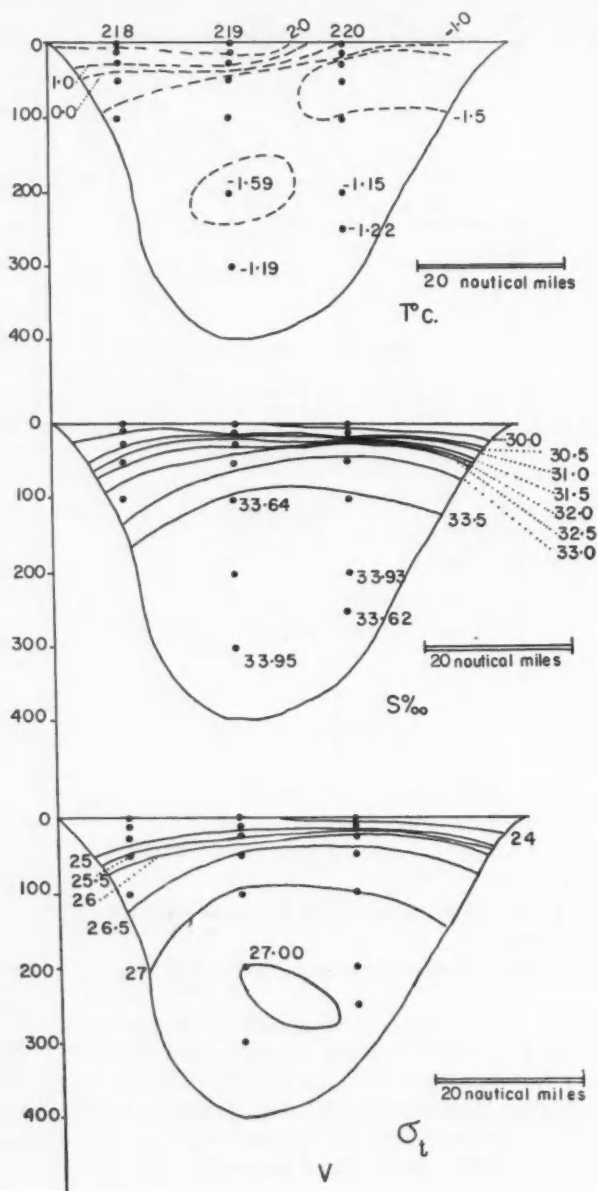


FIG. 12. Temperature, salinity and density profiles, Section V.

familiar pattern of movement in the strait. There is a northwesterly set along the Baffin Island coast, and a southeasterly set along the Quebec shore. The observations were made on the night of July 30-31, 1950. The rise in temperature at 200 m. and below, accompanied by high salinities, is characteristic of Hudson Strait, Ungava Bay and Cumberland Sound, and is subsequently discussed under Temperature-Salinity Correlation.

#### FROBISHER BAY (Sections VII-X, Fig. 13-16)

These sections were run on the following dates: Section VII, August 8, 1951 (Station 320 on August 11, 1951); Section VIII, August 13, 1951; Section IX, August 19, 1951; Section X, August 30, 1951.

Frobisher is a narrow bay with a maximum tidal range at its head of 36 feet. Turbulent conditions, and a hydrodynamic situation dominated by the tides, are therefore to be expected. Section VII, for instance, at the mouth of the bay, shows water entering the bay at the surface on the southwest side and leaving it on the northeast side, the reverse of the normal expected movement. The dominant movement shown by the isopycnals over the section as a whole is outwards from the bay. This can only be explained by the fact that at the time of the observations the tide was flooding at Station 314 and ebbing at both 315 and 320. Similarly in Section VIII, the dominant movement is into the bay, and here Stations 323 and 324 were occupied during the flood tide, Station 325 during the ebb, one hour after high water.

Section X obeys the same rule; both Stations, 338 and 339, were occupied during the ebb tide, and the isopycnals show water leaving the bay. Section IX, however, is an apparent exception to this pattern; both Stations, 327 and 328, were occupied on the ebb tide according to the tide tables, and yet the section shows marked movement inwards. Station 327 was made 2 hours after high water, and this time is in agreement with the actual observation of the time of high water before leaving anchorage on the southwest shore. Station 328, estimating from the tide tables, was occupied 5 hours and 40 minutes after high water. If the assumption of the dominance of tidal currents in Frobisher Bay is correct, this anomaly must be left for the time being as unexplained. The tides of Frobisher Bay have not been given much study up to the present, in fact the very nature of the tidal wave in this region is not certain, and it may well be that the very uneven bottom configuration at the level of Section IX causes local aberrations in the tides. Apart from this one section, however, the agreement between the state of the tide and the slope of the isobaric surfaces is striking. A similar interpretation could well apply to the undulant profiles in Ungava Bay, described above.

As Trites (1956) has pointed out, the dynamics of inshore and partly enclosed waters are not properly understood. Studying the circulation in Chatham Sound, B.C., Trites found an association between the state of the tide and certain aspects of the behaviour of the water; and the reversal of the geopotential slope by the ebb and flow of the tide, in inlets, is illustrated and discussed by Sverdrup, Johnson and Fleming (1942, pp. 557-558).

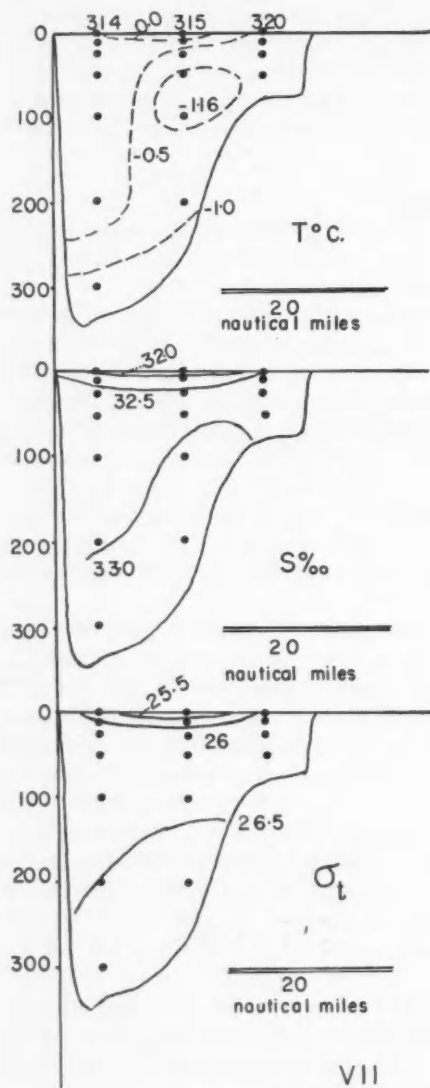


FIG. 13. Temperature, salinity and density profiles, Section VII.

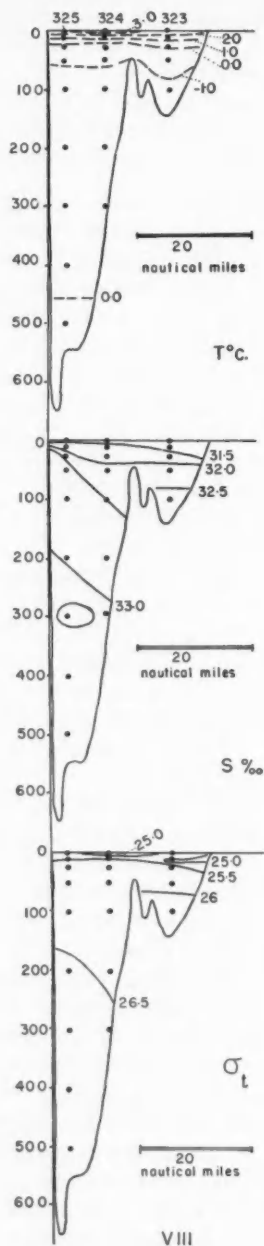


FIG. 14. Temperature, salinity and density profiles, Section VIII.

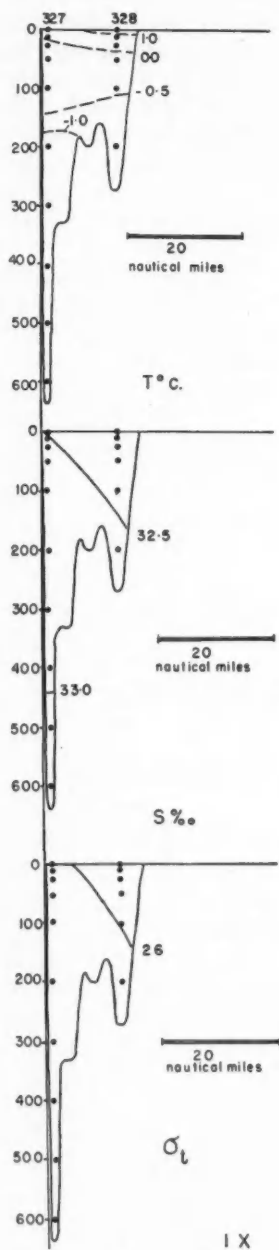


FIG. 15. Temperature, salinity and density profiles, Section IX.

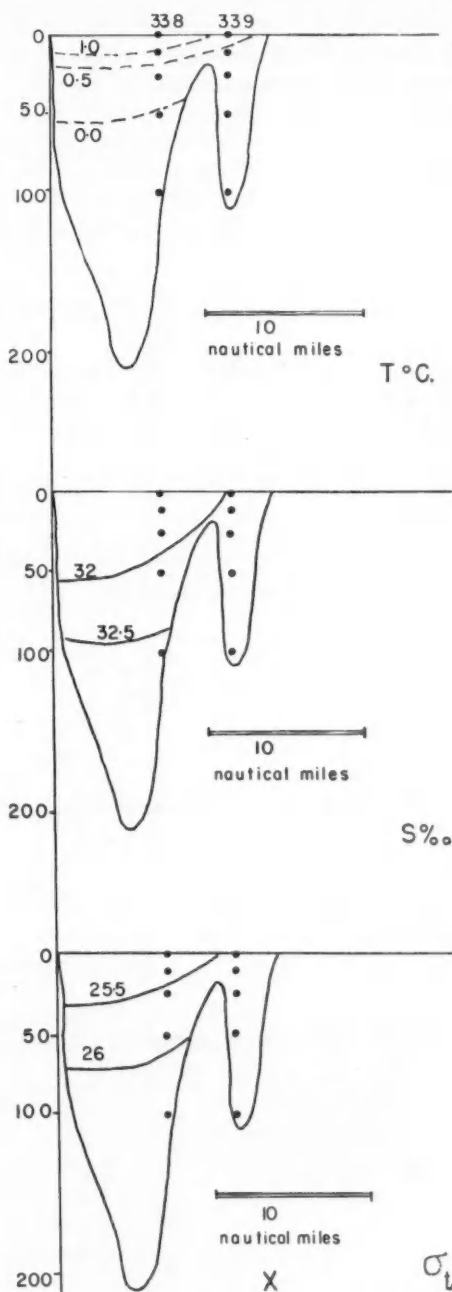


FIG. 16. Temperature, salinity and density profiles, Section X.

## CUMBERLAND SOUND (Section XI, Fig. 17)

Section XI shows water flowing both in and out of the sound, at different levels, for the most part very weakly. This again may be associated with the

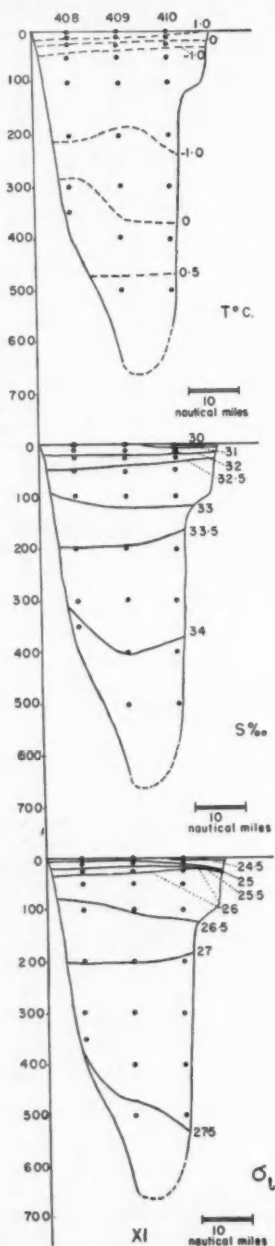


FIG. 17. Temperature, salinity and density profiles, Section XI.

tide, for Stations 408 and 410 were occupied over slack water, the former at high water and the latter at low water. The 300- and 350-m. samples at Station 408 were taken during the end of the flood, about half an hour before high water, while the 10-, 25- and 50-m. samples were taken half an hour after high water. These times are in agreement with the slopes of the isopycnals at the depths mentioned. Similarly, the indication of inward flow between Stations 409 and the northeast shore agrees with the state of the tide (beginning to flood) at the time of taking the 0-, 10-, 25- and 50-m. samples at Station 410. The section was run on the night of July 30-31, 1952.

NORTHERN HUDSON BAY AND WESTERN HUDSON STRAIT (Sections XII-XVII, Fig. 18-23)

All these were run in the 1953 season. The dates of observation are as follows: Section XII, July 24; Section XIII, July 25; Section XIV, August 3 (Station 520 on August 4); Section XV, August 5; Section XVI, August 11; Section XVII, September 2.

Section XII shows the expected southward set between Station 506 and the

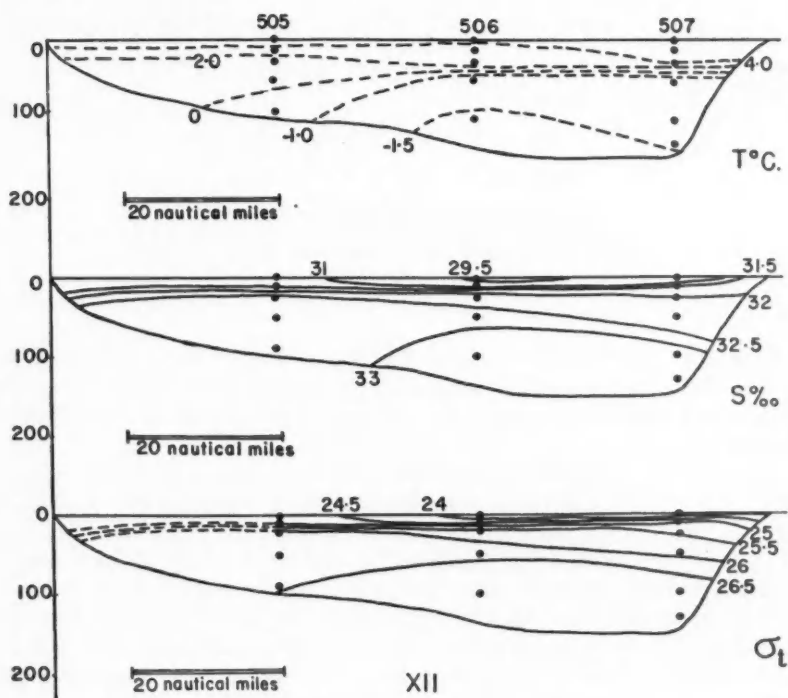


FIG. 18. Temperature, salinity and density profiles, Section XII.

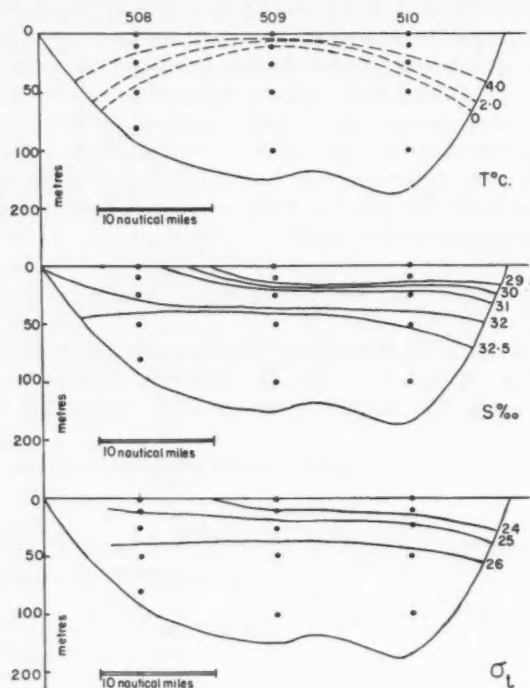


FIG. 19. Temperature, salinity and density profiles, Section XIII.

mainland coast; it is well developed below 50 m. between Stations 506 and 505, but of uncertain strength farther west, owing to the absence of an inshore station. A weak northward movement is indicated between Station 506 and Southampton Island, below 25 m.

Section XIII, between Southampton and Coats Islands, shows only northeasterly movement in Fisher Strait. Whether this is a permanent condition is uncertain. In an earlier paper (Dunbar, 1951) I suggested that there might be a southwesterly set in this region, based on the drift-bottle results of the *Loubyrne* expedition of 1930 (Hachey, 1935). The present results, however, and the statements in the Arctic Pilot, Vol. III (British Admiralty, 1947), indicate that such a southwesterly current is not normal. The point is not unimportant, since it has considerable relevance to the fate of the water which flows southward past Seahorse Point, eastern Southampton Island (see below).

A weak movement into the bay, however, is shown in Section XIV, between Station 516 and Coats Island. Taken together with the previous section, this



indicates a clockwise rotation round Coats Island. At the eastern end of Section XIV there is a northerly current leaving Hudson Bay, between Station 517 and Mansel Island. In Section XV, unfortunately, there is no station close enough to Mansel Island to demonstrate whether or not a similar circulation occurs round that island as round Coats. A southward set along the east coast of Mansel Island, which would be implied by such a rotary current, is, however, described in the Tide Tables for 1957: "... Captain Balcom of the Government steamer *N. B. McLean* reports a predominant southward set along the eastern side of Mansel Island". For the rest, Section XV shows a northward set between Station 521 and the Quebec coast, but only below 25 m.

Between the Quebec coast and Salisbury Island, Section XVI shows only water moving to the east, out of Hudson Bay, with the exception of an indication

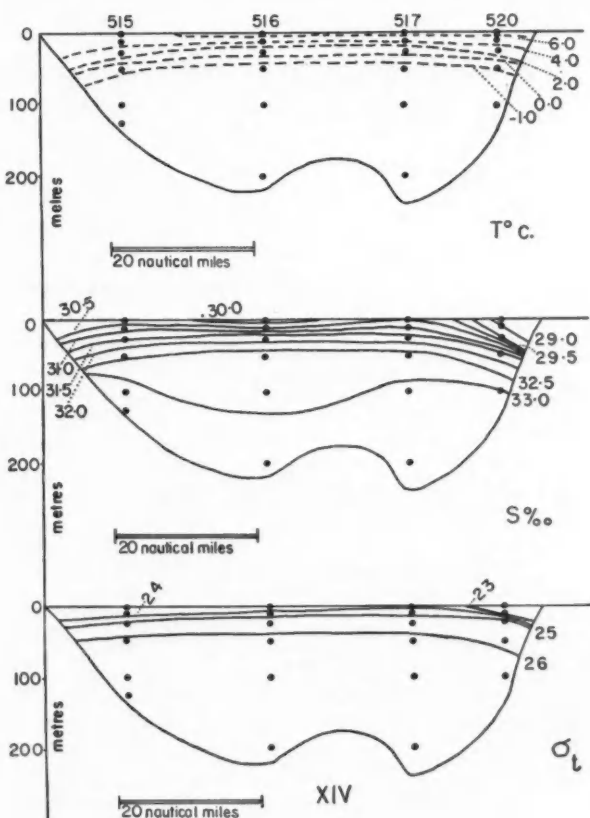


FIG. 20. Temperature, salinity and density profiles, Section XIV.

of westward movement at the 200-m. level at Station 531, close to Salisbury Island, where the 26.7 isopycnal surface curves downward.

In Fig. 23, Section XVII is presented from the northwest or Foxe Basin side, with Baffin Island on the left and Southampton Island (Seahorse Point) on the right. There is a well-developed current setting into Foxe Channel along the Baffin Island coast between that coast and Station 544, and a lesser current setting out of Foxe Channel along the Southampton Island coast. This latter current was also found, by various methods of measurement, by the H.M.C.S. *Labrador* expedition of 1955 (Campbell and Collin, 1956). In view of the fact that there is little evidence of a westerly set in Fisher Strait (see above), this water must find its way elsewhere, probably joining the water leaving Hudson Bay through Section XVI.

The surface currents demonstrated by Sections XII–XVII are shown in Fig. 24, together with the distribution of temperature and salinity at the surface

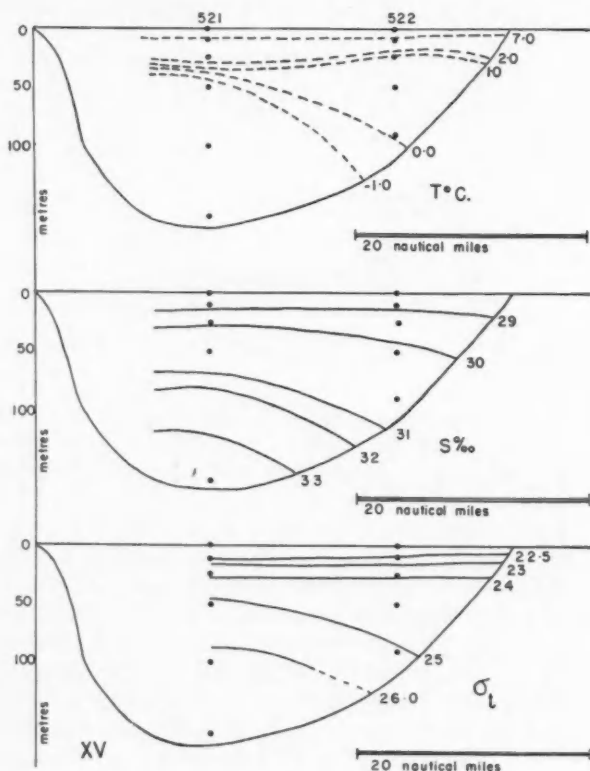
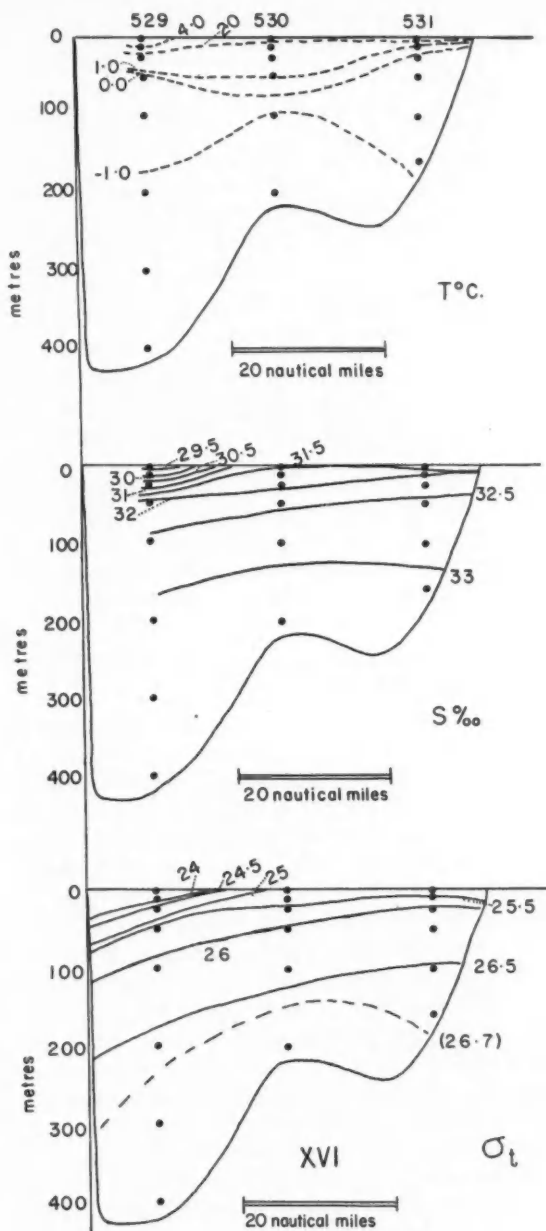


FIG. 21. Temperature, salinity and density profiles, Section XV.



22. Temperature, salinity and density profiles, Section XVI.

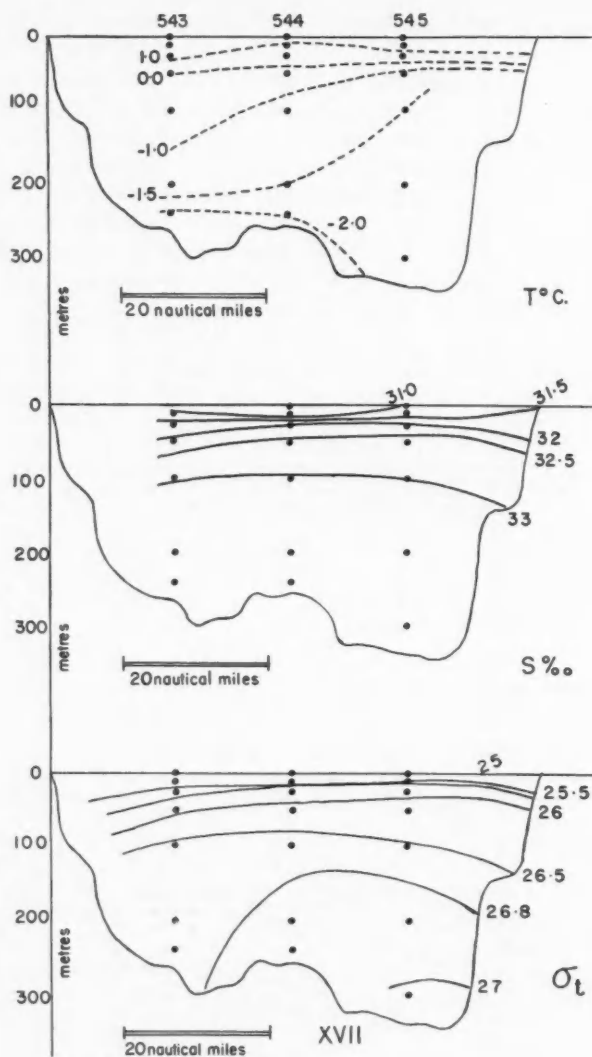


FIG. 23. Temperature, salinity and density profiles, Section XVII.

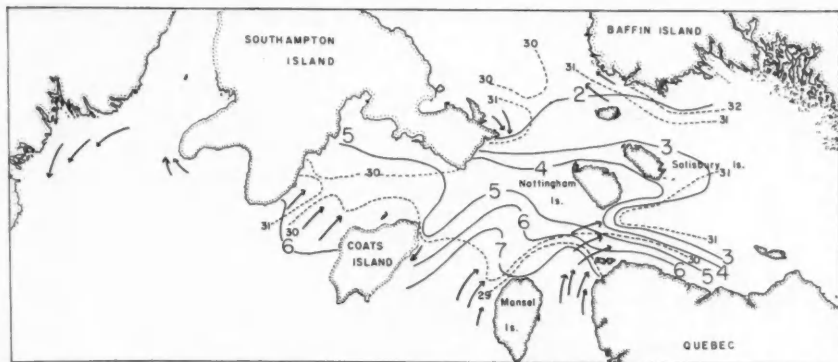


FIG. 24. Surface temperatures, northeast Hudson Bay, late July to early September, 1953. Arrows show surface currents as indicated by Sections XII to XVII.

in this region, for late July to early September, 1953. The strong warming and freshening effect of the outflow from Hudson Bay is well shown. The chart is more detailed than the *Loubyrne* figures for 1930 (Hachey, 1931) and shows a somewhat greater extension of the warmer surface water towards the northeast, although the season of observation of the two expeditions is the same.

#### TEMPERATURE-SALINITY CORRELATION (Fig. 25-32)

The chief interest that attaches to the T-S correlation figures is the presence or absence of a turn-up of the curves in the deeper water, indicating the intrusion of a water of origin different, or partly different, from that of the remainder of the water, which consists of Arctic water considerably diluted in the upper 50 m. by land drainage run-off and melting ice. This turn-up occurs commonly at 100 m. and below in Ungava Bay (Fig. 25), mid-Hudson Strait (Fig. 26) and Cumberland Sound (Fig. 28), but it is almost entirely absent from Frobisher Bay (Fig. 27) and Hudson Bay and the western end of Hudson Strait (Fig. 29). Similar T-S curves are recorded from the Labrador Current (Bailey and Hachey, 1951a), but not from the Labrador fjords or the inshore regions of that coast (Nutt and Coachman, 1956; Nutt, personal communication). In the Labrador Current this rise in temperature in the deeper water is caused by admixture either of the deeper water of the Canadian Current (Baffin Island Current), or of water from West Greenland, or of Labrador Sea water. In Cumberland Sound, Hudson Strait and Ungava Bay, the intrusion of water direct from the Labrador Sea core water is improbable. Whether the influence comes from the West Greenland current, part of which turns westward towards the Canadian coast in the region of the Holsteinsborg Ridge, or from the Baffin Island Current, is uncertain; in either case part of the water probably comes ultimately from the West Greenland side. The temperature levels reached by the upturned portions of the curves

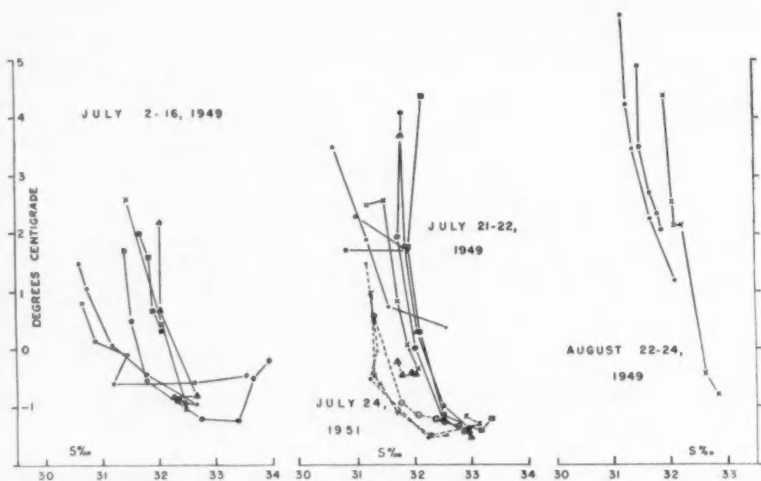


FIG. 25. Temperature-salinity curves, Ungava Bay.

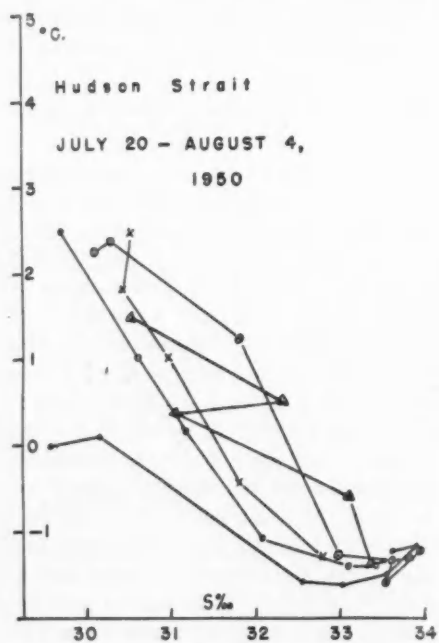


FIG. 26. Temperature-salinity curves, mid Hudson Strait, 1950, from Stations 208A, 218, 219, 220 and 221.

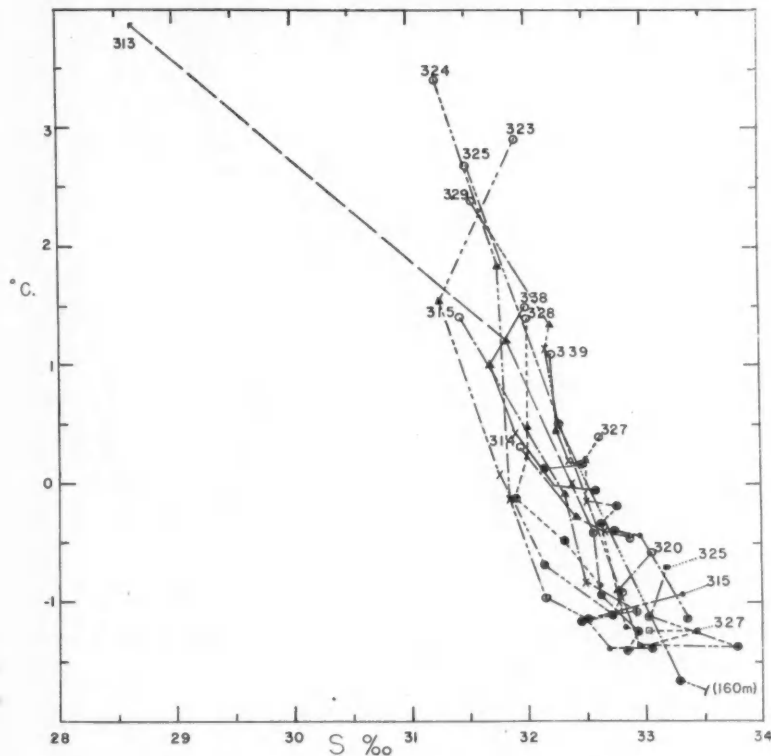


FIG. 27. Temperature-salinity curves, Frobisher Bay, 1951. Numbers are station numbers. Depth symbols as in Fig. 28.

(between  $-1.0$  and  $0.0^{\circ}\text{C}.$ ) are low, indicating that the proportion of West Greenland water is not overwhelming; the effect is more marked in Cumberland Sound than elsewhere in the region studied here.

The almost complete absence in Hudson Bay of this intrusion from the Atlantic region is not surprising, but it is interesting in view of earlier discussions of a possible marine climatic change in Hudson Bay owing to Atlantic influence (Dunbar, 1951; Bailey and Hachey, 1951b). On the present evidence such Atlantic influence is very slight, perhaps intermittent. Figure 29 shows minor upturnings at four Stations, 516, 521, 527 and 544. Figure 31 (1954) shows one at Station 612. The rises in temperature are all quite small, and the shapes of the curves as a whole are not the same as in Cumberland Sound and Ungava Bay. Whether these can be interpreted as the last depauperate traces of Atlantic water is a matter of opinion. Since the Atlantic influence elsewhere appears only below the 100-m. level, and is most marked still lower down (as in Cum-

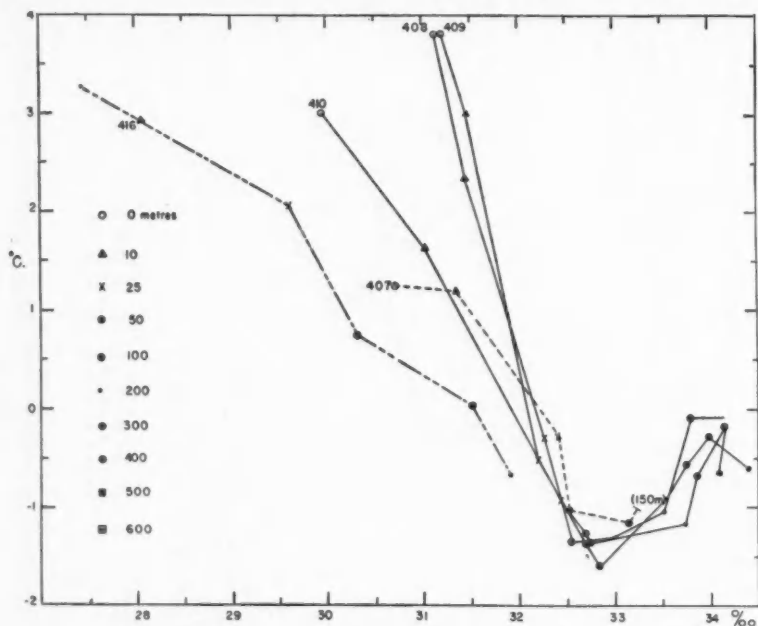


FIG. 28. Temperature-salinity curves, Cumberland Sound, 1952. Depths symbols apply also to Fig. 27, 29 and 31.

berland Sound), the very shallowness of Hudson Bay may exclude much of the Atlantic water.

From Fig. 27 it appears that the Atlantic intrusion is as slight in Frobisher Bay as it is at the exit from Hudson Bay. This, in view of the strong effect at the mouth of Cumberland Sound and the considerable influence in Hudson Strait and Ungava Bay, requires to be accounted for. The upturning appears at three stations only, 315, 325 and 327, and at all three they are associated with density inversions (see below), so that they cannot be considered as indicative of the Atlantic effect. The Cumberland Sound section (Fig. 28) shows increase in temperature, without density inversion, between 100 and 400 m.; the threshold at the mouth of Frobisher Bay has a sill depth of about 300 m. There should therefore be no obstacle to the entry into the bay of large quantities of the warmer water below 100 m.

A possible explanation of this anomaly can be found by examining the positions, on the T-S graph, of the 100- and 200-m. datum points. These are compared, Frobisher Bay with Cumberland Sound, in Fig. 30—Stations 329 and 416 have been omitted, since they lie in small fjords of special hydrographic conditions (see below). The separation of the two sets of datum points is quite clear, the more so if the 100-m. points of Frobisher are compared with those from Cumberland, and the same for the 200-m. points. Apparently the turbulence



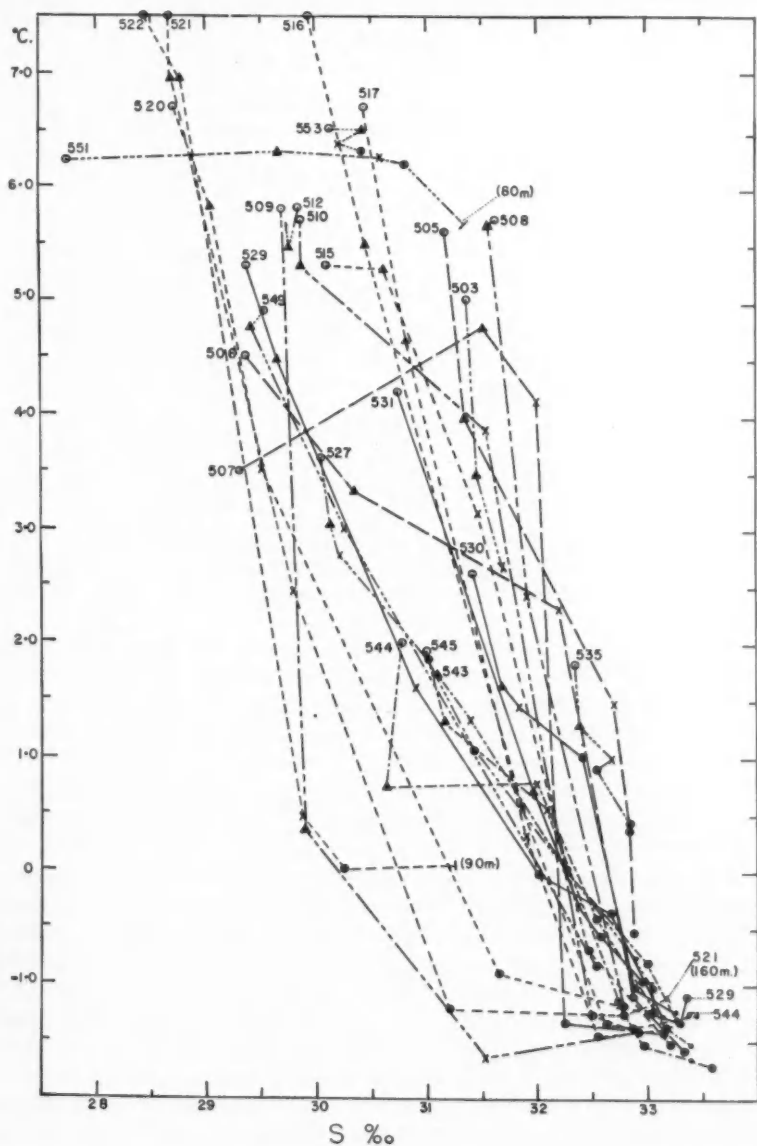


FIG. 29. Temperature-salinity curves, northeast Hudson Bay, 1953 (Sections XII to XVII and isolated stations). Depth symbols as in Fig. 28.



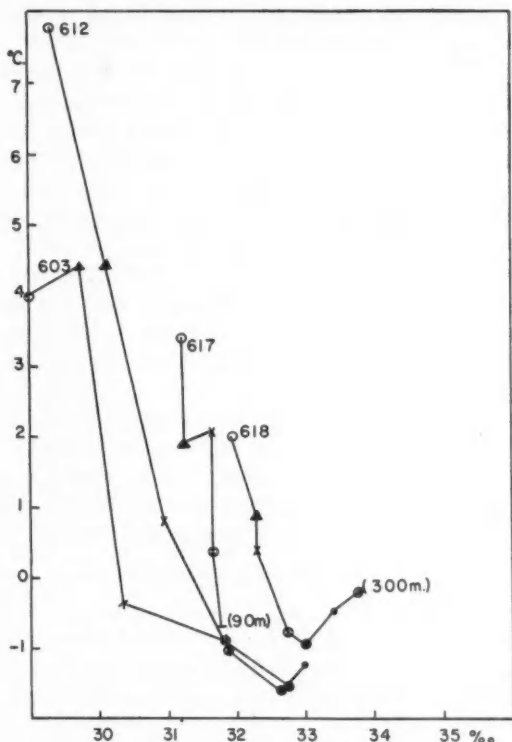


FIG. 31. Temperature-salinity curves for two stations in northeast Hudson Bay (603, 612), one in Sugluk inlet (617), and one in northeast Ungava Bay (618), 1954.

between water east and west of Akpatok, the Atlantic influence being more strongly developed in the northeastern part of Ungava Bay than elsewhere within the bay.

There are three more points to be observed concerning the T-S correlations from Hudson Bay. In Fig. 29, the different types of line (dotted, full, etc.) represent the several hydrographic sections. There is a separation of the curves involving a salinity of approximately 2‰ in all but the bottom right-hand corner of the Figure, which might be thought to be significant of some major dichotomy of water type. This separation, however, on inspection, turns out to exist in the upper 50 m. only (with one exception—90 m. at Station 522), and can therefore safely be put down either to local turbulence in the upper layers, or to the dynamic pattern of the movement of the water itself, or to coastal effects. For instance, five of the stations which show the shift to the left—520, 522, 521 (Section XV and the eastern end of Section XIV), 527 and 529—are all at the northeastern

corner of Hudson Bay, in the main outgoing current, where lower salinities and densities are to be expected.

The second point is the surprisingly high temperature from surface to bottom (80 m.) shown at Station 551. Station 551 is close to the western end of Section XII, but whereas that section was run on July 24, 1953, Station 551 was occupied on September 11 of the same season, some 7 weeks later. The same high temperatures are shown at Station 553, farther down the coast, to a depth of 50 m. Whatever the causes of these temperatures, they would be expected to be quite important biologically; further work along this coast is clearly needed, particularly in connection with (1) the known existence in Hudson Bay of relics from a warmer climate (Dunbar, 1955a) and (2) the experiment already under way to introduce species of Pacific coast salmon into streams draining into southwestern Hudson Bay. The high temperatures are most probably the result of intense insolation coupled with wind-mixing.

Finally, there is the question of long-term changes in the marine climate of Hudson Bay. Bailey and Hachey (1951b) and Dunbar (1951) have suggested the possibility of an increasing Atlantic influence in Hudson Bay, on the basis of a comparison of the *Loubyrne* 1930 results with those of the *Haida* in 1948. This is illustrated in Fig. 32, in which polygon A encloses all datum points from the

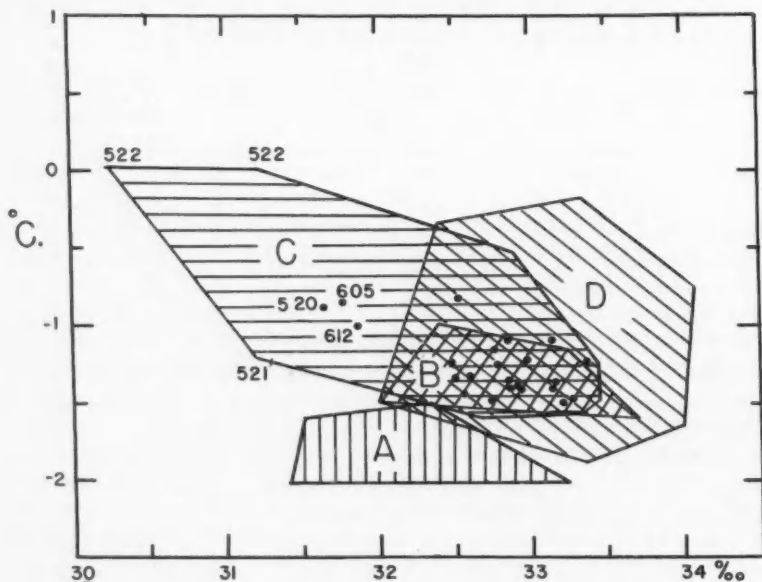


FIG. 32. Polygons enclosing temperature-salinity datum points for *Loubyrne* observations, 1930, in Hudson Bay (A); *Haida*, 1948, Hudson Bay (B); *Calanus*, 1953-54, Hudson Bay (C); and Arctic water in general, from Dunbar (1951). In all cases observations from depths less than 50 m. are omitted.

1930 expedition from 50 m. down to the bottom, and polygon B encloses the equivalent observations from 1948. For comparison, polygon D represents the Polar, or Arctic, water of the eastern Arctic in general, taken from the upper 200 m. in various regions supposedly outside the influence of Atlantic water (see Dunbar, 1951). Although the extreme low temperatures recorded from several stations in 1930 have been questioned, as possibly due to instrumental difficulties, nevertheless the general low level of the 1930 temperatures as compared with 1948 must be considered significant, and moreover, the differences in salinities between the two years' results are even more striking. Polygon C in Fig. 32 encloses the *Calanus* results from the 1953 and 1954 seasons, again with all observations from depths less than 50 m. excluded. These come from the north Hudson Bay only, between the islands, and not from the main body of the bay, but the *Calanus* stations nevertheless fall in regions covered by both the *Loubyrne* and the *Haida*. The datum points in polygon C which fall significantly outside the *Haida* 1948 polygon, marked by the station numbers, are all from 50 m. depth with one exception, a 90-m. observation at Station 522. It is reasonable to ascribe these lower salinities and higher temperatures to local and temporary conditions, and since the bulk of the *Calanus* observations fall within the *Haida* range, it can safely be stated that there is here no evidence of climatic change since 1948.

#### DENSITY INVERSIONS

Inversions of density in the sea have not yet achieved scientific respectability; and it must be stated from the start that any forces tending to invert must also tend to bring about mixing and therefore an approach to uniform density. This is undoubtedly a correct view to take, but it must nevertheless be admitted that the dynamics of turbulence are by no means fully understood and that the time scale involved in the mixing process is not known. Moreover, density inversions are nothing new; they have appeared in the results of several oceanographic expeditions, and it is not unreasonable to suspect that they would have appeared far more frequently had they not been quietly obliterated by a stroke of the pen, on the assumption that they were mistakes of one sort or another. Such instabilities, in fact, have usually been looked upon as fictitious, attributed to faulty thermometers, to errors in thermometer readings, sample labelling, titration, or the working up or filing of results.

The earliest instance of density inversion of which I am aware is in the late nineteenth century, from the results of the cruise of the *Vitiaz* in the Okhotsk Sea (Makaroff, 1894). That was before the days of standardized oceanographic method, and might be disqualified also on the grounds of thermometer error. The next is from the results of the *Michael Sars* expedition of 1910, in the north Atlantic (Helland-Hansen, 1930, and quoted in Sverdrup, Johnson and Fleming, 1942, p. 417). Spilhaus, Ehrlich and Miller (1950) have recorded inversions of density in the waters just south of Cape Cod, and have given evidence of some correlation of the times of observed instability with the times of lunar transit. In his extensive study of the Faroe-Shetland Channel, Tait (1957) found more

or less persistent instabilities; he writes: "One effect of turbulence which is encountered in the Faroe-Shetland Channel is inversion of density in the vertical column, and yet another, in at least one particular case, is the suggestion of a horizontal sub-surface tortional current through the body of the oceanic water-mass." That density inversions might be set up by tortional currents appears to be a new idea, and might have considerable relevance to the problem of the inversions found by the *Calanus* expeditions.

The observations of the H.M.S. *Challenger* off the Labrador coast in 1932 contain five stations with density inversions (British Admiralty, 1932), and the *Haida* in 1948 also recorded five inversions, at its Stations 3, 11, 13, 14 and 25. One of these stations was off the Labrador coast, two were in Hudson Strait and two off the coast of Coats Island. Four of them were between the surface and 10 m. depth. Finally, Dr. Carsola (personal communication) states that density inversions of short duration are common in shallow water observations in progress (1954-55) at the U.S. Navy Electronics Laboratory at San Diego.

In the instances recorded by the *Calanus*, titrations have been repeated where possible, and the methods used on board ship have been strictly examined and seem to preclude the possibility of other errors. Had there been errors in titration, it might be expected that although the salinities showed inversion, the temperatures would not. Of the total 27 instances used here (see below: some did not depend on depth observations taken simultaneously, and have been excluded), there are found to be eight involving temperature inversions as well as salinity inversions, two in which the temperature was the same at the two levels involved, and 17 in which there was no temperature inversion. Of those 17, however, there was a temperature inversion in eight instances at the level immediately above or below the density inversion. Copies of the raw data can be examined upon request to the author.

Unstable conditions of the type discussed here were recorded at 24 stations by the *Calanus* expeditions of 1949 to 1953. There were two inversions at Station 221 and three at Station 327. In the record given in Table I, only cases of inversion which involve "simultaneous" measurement of temperature and sampling of the water at the two depths involved are included; that is, where the depth levels were spanned by a single string of samplers, closed and reversed in series. The actual time difference between observations 100 m. apart is about 30 seconds, and between other vertical distances in proportion. There were a few instances of inversion, mentioned below, which were based on measurements made many minutes apart following separate lowerings of the wire. These have not been included in the statistical treatment.

The figures in the last column of Table I are measures of stability, in these cases negative stability, calculated from the formula

$$E = 10^5 (d\sigma_t/dz)$$

(Sverdrup, Johnson and Fleming, 1942), where  $d\sigma_t$  is the difference in density between the two depth levels concerned, and  $dz$  the difference in depth in metres.

TABLE I

Station	Date	Depth of Inversion	Time of observation	Time of high water	Time before or after high water	Stability (see text)
		<i>m.</i>	<i>EST</i>	<i>EST</i>	<i>hr. min.</i>	
103	16/7/49	100-200	0315	2330	3 45 after	-290
118	22/7/49	10-25	0545	0530	0 15 "	-5730
220	31/7/50	200-250	0140	2053	4 47 "	-480
221	4/8/50	10-25	1100	1230	1 30 before	-6870
221	4/8/50	200-250	1020	1230	2 10 "	-660
201C	29/8/50	50-80	1100	0900	2 00 after	-600
305	24/7/51	10-25	0920	1230	3 10 before	-533
306	24/7/51	200-275	1415	1240	1 35 after	-267
308	24/7/51	25-50	2120	0055	3 35 before	-280
309	28/7/51	100-150	1930	1600	3 30 after	-180
314	8/8/51	50-100	0840	1020	1 40 before	-240
315	8/8/51	50-100	1125	1020	1 05 after	-680
320	11/8/51	10-25	1420	1247	1 33 "	-200
325	13/8/51	300-400	1548	1517	0 31 "	-610
327	19/8/51	50-100	1116	0820	2 56 "	-240
327	19/8/51	300-400	1030	0820	2 10 "	-70
327	19/8/51	500-600	1045	0820	2 25 "	-340
328	19/8/51	25-50	1353	0820	5 33 "	-250
329	21/8/51	10-25	1022	0956	0 26 "	-133
339	30/8/51	50-100	0750	0530	2 20 "	-520
410	31/7/52	400-500	0420	2228	5 52 "	-90
508	25/7/53	50-80	1625	1229	3 56 "	-100
509	25/7/53	50-100	1845	0060	low water	-240
512	8/9/53	10-18	1430	1238	1 52 after	-750
535	17/8/53	25-50	1134	1513	3 39 before	-360
543	2/9/53	200-240	0715	0624	0 51 after	-125
544	2/9/53	200-240	1105	0632	4 33 "	-100

With the exception of the inversions in the upper layers at Stations 118 and 221, the indices of instability are not large compared with the positive stabilities found normally in these waters in summer. The force required to produce the instabilities must nevertheless be considerable. The most obvious, in fact the only, force that could reasonably be expected to play a part in this phenomenon is to be found in the large tidal ranges and currents which characterize the bottle-neck region of Ungava Bay, Hudson Strait, and Frobisher Bay. Accordingly, the distribution of the times of observation of the inversions with respect to the state of the tide was first compared with hypothetical distributions in which the same number of stations were modally arranged about points from 2 to 3 hours after or before high water, on the hypothesis that the inversions tended to occur close to the time of strength of tide, whether the tide was rising or falling. Agreement with these distributions was unsatisfactory. The stations at which inversions occurred were then arranged on a tidal clock, the period of the clock being 12½ hours (Fig. 33).

Preliminary published notice of this analysis has already been given (Dunbar, 1955b). Three instances of inversion based on "non-simultaneous" observations were included in that preliminary report by oversight, and they have here been removed. Figure 33, then, shows the distribution, with respect to the state of the tide, of 17 stations at which inversions were observed in Ungava Bay, Hudson Strait and Frobisher Bay, 1949-51, compared with the remainder of the stations

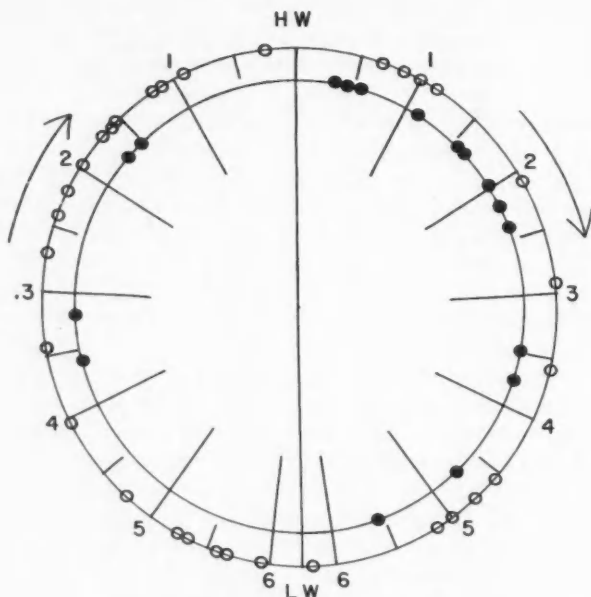


FIG. 33. Tidal clock showing the state of the tide at the time of occupation of stations with density inversions (black) and without density inversions (open circles), in Ungava Bay, Hudson Strait and Frobisher Bay, 1949-51. HW—high water; LW—low water. Figures are hours.

occupied during the same seasons and in the same area. The total number of stations is 48.

To test the agreement of these stations on the tidal clock with an even distribution, ten classes of radial scatter, each consisting of a sector subtending an angle of  $36^\circ$  at the centre of the clock, were set up, and the degree of association was tested by the  $\chi^2$  method. Comparing the radial scatter of all stations with the equally distributed radial pattern for the same total number of stations gave a  $P$  value of .57. For the stations without inversions, the  $P$  value was .56. These are both close to an equal scatter, as would be expected. The  $P$  value for the stations with density inversions, on the other hand, is .08, which is fairly close to disagreement with the equal scatter at the 5% level. Moreover, a comparison of the means (standard error of the difference between the means) of the inversion and non-inversion stations gives a  $P$  value of .01 (difference of the means is 2.78 times its standard error), which is evidence of significant disassociation. It is, furthermore, immediately apparent that of the 17 inversion stations 13 lie on the ebb tide and over one half lie in one quadrant in the first three hours after high water.



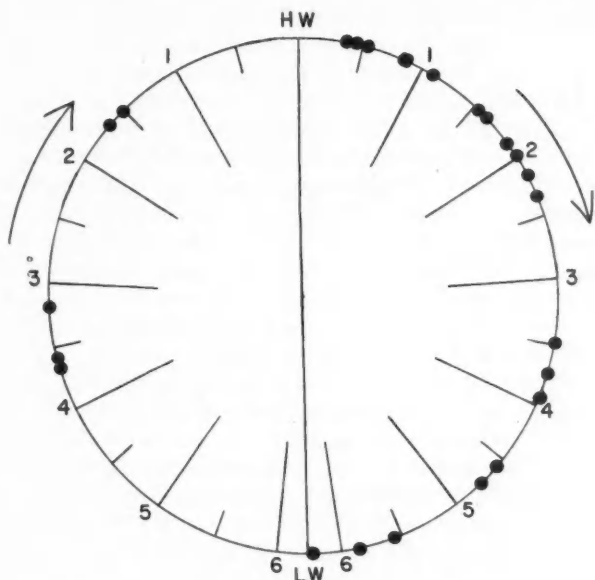


FIG. 34. The same as in Fig. 33, but showing the stations without density inversions omitted and seven stations with density inversions added, from the 1952 and 1953 seasons (Stations 410, 508, 509, 512, 535, 543 and 544).

In the years 1952 and 1953, seven more observations of instability were made, as shown in Table I, one at the mouth of Cumberland Sound, one off Cape Dorset, two in Foxe Channel and three in Fisher Strait. These are added to the earlier observations in Fig. 34. When this distribution is compared with an even scatter of the same number of stations (24), again by  $\chi^2$ , the value of  $P$  is a little less than .04 (about .038), again good evidence of disassociation from the even scatter. In this Figure, all but five of the stations lie on the ebb tide, and 11 of the 24 lie in the first three hours after high water.

On the hypothesis that the inversions are associated not only with the state of the tide but with the force of the tidal wave, it is interesting that in spite of the large number of hydrographic stations occupied in 1953 in northern Hudson Bay, there should be so few instances of instability as compared with the observations in Hudson Strait, Ungava Bay and Frobisher Bay. In fact, of the seven instances from the 1953 season, only three can be said to come from Hudson Bay itself. This is in keeping with the smaller tidal ranges within Hudson Bay than in the rest of the area studied here. There were no instances of instability recorded from the few stations in Hudson Bay occupied in 1954.

The inversions at Stations 543 and 544 have been included in Table I. The temperatures from which the densities are calculated at these two stations, at 240 m., are  $-2.08$  and  $-1.99$  respectively; values which are of the order found by Hachey (1931) in Hudson Bay in 1930, and also by H.M.C.S. *Labrador* in Foxe Basin in 1955 (Campbell and Collin, 1956). These very low temperatures may be caused by thermometer inaccuracies; and where they have been met in the *Calanus* work the temperature has been measured again at the same depth with a different thermometer. In the case of Stations 543 and 544, the second thermometer readings were  $-1.39$  and  $-1.57$  respectively. Unfortunately salinity samples were not taken together with the second temperature measurements. However, if the higher temperature value had been used together with the salinity from the first observation in each case, the densities would have been lower, so that the density inversion would have been more marked, not less so.

There are nine stations at which instabilities appear but at which these may be artifacts because the observations at the two depths concerned were not made at the same time (with a single string of samplers). These instances are set out in Table II, in which the first seven represent instabilities between the surface and 10 metres, the remaining two being from various depths lower down.

TABLE II. Time of observations, before (+) or after (-) high water.

Station	Hours	Minutes
227	+0	15
323	+3	30
327	-3	15
338	-1	10
508	-3	56
544	-4	00
549	-3	24
219	-2	15
553	-3	45

Although these instances are not taken as valid for present purposes, it is at least interesting, if not more than interesting, that eight out of the ten occur on the ebb tide.

It must be admitted that the level of accuracy possible at present in the calculation of the state of the tide at all stations may not be as great as could be desired. The tide datum points are too far apart to admit great accuracy in the tracing of the progress of the tidal wave. However, by checking the times calculated from the tide tables against observations on shore as soon as possible before or after occupying hydrographic stations, it has been possible to gain considerable confidence in the estimates; the errors are probably of the order of considerably under one hour in some cases, much less in others. Errors of this order would not disturb the general pattern of the results.

The conclusion is that there is a turbulent effect associated with the tide,

particularly with the ebb tide, whose time scale is not known but which results in frequent finding of density inversions when the column of water is sampled in the standard way at standard depths, in areas where the tidal range is large and the tidal currents are consequently strong. Such turbulence would be expected to have important biological effects, among others, and indeed such effects have already been recorded in the vertical distribution of the microplankton (Bursa, personal communication). Such instabilities are also extremely interesting from the physical point of view, and would repay further and much more detailed investigation. As already mentioned, the tortional current effect recorded by Tait (1957) in the Faroe-Shetland Channel might be a profitable line of attack on the problem.

The maximum tidal ranges involved (at springs) are as follows: Head of Frobisher Bay (Frobisher's Farthest), 36 feet; Port Burwell, 22.5 feet; Koksoak River entrance (Ungava Bay), 45 feet; Leaf Basin (Ungava Bay), 54.5 feet; Lake Harbour (southern Baffin Island), 35 feet; Wakeham Bay, 30 feet; Nottingham Island, 15.75 feet.

One further point of interest is that in Frobisher Bay some of the inversions were found at depth levels between 300 and 600 m. In view of the fact that the distribution in depth of tidal currents in inlets is little known (e.g. Pickard, 1953b), this might have a possible value in the study of tides as such.

#### VERTICAL STABILITY

Since some time has been devoted here to the study of negative stabilities, it might be proper to give some account of the general stability conditions in the regions covered by the present series of expeditions. Table III sets out the values of the approximate stability index  $E$  for a number of stations from the whole geographic range from northwest Hudson Bay to Cumberland Sound, representative of the stations occupied in the 1947-54 seasons. (One 1947 station, No. 41 in Ungava Bay, is included in this series.)

It will be seen first that with two exceptions the negative stabilities given in Table I are all small compared with the general range of positive stabilities shown in Table III. This has already been referred to above.

Five other points which should be mentioned here are shown in Table III. (1) The order of stability everywhere in this area is considerably higher than is found in temperate regions, for instance in the North Atlantic. This is characteristic of northern, especially Arctic, waters in summer. (2) The upper 50 m. in Hudson Bay are somewhat more stable than elsewhere in the area, and to some extent this greater stability extends down to 100 m. (3) Stabilities in Hudson Strait, Ungava Bay, Frobisher Bay and Cumberland Sound are of the same order throughout. (4) The contrast between the Hudson Bay stations and the rest is not very great, except at the 25- to 50-m. level. (5) The columns of equal density between the surface and 10 m. at Station 115, and between 25 and 100 m. at Station 109, point to mixing processes, probably the result of density inversion some short time before the measurements were made.

TABLE III. Stabilities,  $10^6(ds_t/dz)$ , for sample stations in the area covered (1947-1954)

TABLE III. Stabilities, $10^4(\sigma\epsilon_1/\sigma\epsilon_2)$ , for sample stations in the area covered (see Fig. 1).																											
Depth	Stn: 505 Date: 24/7	509 25/7	603 24/7	612 10/8	516 3/8	521 5/8	530 11/8	545 2/9	220 31/7	309 28/7	208A 20/7	115 21/7	128 24/8	307 31/8	234 17/8	41 16/7	108 16/7	109 21/8	618 8/8	314 13/8	324 13/8	409 31/7					
m.																											
0	3000	5800	6000	10400	6600	900	1900	1600	4800	12000	8400	0	1900	4400	1200	-100	1500	6300	3400	4100	5600	2600					
10	8470	9130	5330	6200	10200	8800	934	5200	13930	2800	3270	1666	266	1533	600	133	1533	2530	333	1330	1133	5460					
25	720	4520	4640	3280	2680	5200	1920	2320	1600	160	3000	1600	480	1040	1800	1240	3320	0	1600	720	1240	1680					
50		240	1580	1200	400	2560	900	400	800	180	1680	1060	900	200		480	1020	0	440	-240	500	240					
100							320	340	300			150			240	170		300	200	170	540						
200								160								230		260	340	280	160						
300																					150						
400																					310						
500	North and northeast Hudson Bay											West Hudson Strait		Mid-Hudson Strait				Ungava Bay							Frobisher Bay		Cum-ber-ld. Sd

## WINTER RÉGIME IN NORTHERN HUDSON BAY

That Hudson Bay below about 50 m. might be dynamically dead was suggested by Hachey (1931) as a result of the 1930 observations. Later, working on the *Haida* 1948 material, Bailey and Hachey (1951b) found that this was in fact not the case, which is confirmed by the *Calanus* findings reported here (above) for the north and northeastern part of the bay. Another possibility which arose out of the same observation, namely the very high stability of the Hudson Bay water in summer, was that the normal winter vertical exchange of water might be inhibited, and that this might be related to the supposed low biological productivity of the bay. This low productivity was deduced from the lack of commercially valuable fishes, and it is now known that Hudson Bay, in terms of plankton production, is not greatly different from neighbouring bodies of water. The evidence available at present, given here, suggests that this second possibility is also not realized, and that on the contrary the behaviour of the Hudson Bay water in winter, at least in the upper 50 m. (all that we have material from), is normal.

Opportunity to obtain hydrographic observations in winter in Hudson Bay is rare, and a preliminary attempt at Fort Churchill in March was unsuccessful because water of reasonable depth could not be reached at the time. In March 1955, however, Mr. A. W. Mansfield arrived at Coral Harbour, Southampton Island, and was able to obtain temperatures and water samples from the surface to 50 m. during April, May and June. The results are given in Table IV. All the

TABLE IV. Data from winter stations in South Bay, Southampton Island, 1955.

Date	Location	Depth	Temperature	Salinity	Density
		m.	°C.	‰	$\sigma_t$
April 3	63°45'N. 83°02'W.	1	-2.20	32.75	26.38
		10	-1.72	33.19	26.70
		25	-1.75	33.19	26.72
		50	-1.72	33.28	26.80
April 28	63°40'N. 82°40'W.	1	-1.57	32.94	26.52
		10	-1.65	32.94	26.53
		25	-1.73	32.97	26.55
		50	-1.79	33.12	26.67
May 17	63°50'N. 83°25'W.	1	-1.62	32.94	26.52
		10	-1.62	32.94	26.52
		25	-1.77	33.12	26.67
		50	-1.79	33.49	27.05
May 27	63°43'N. 83°37'W.	1	-1.42	33.03	26.59
		10	-1.43	33.06	26.61
		25	-1.64	33.06	26.62
		40	-1.75	33.08	26.64
June 7	63°46'N. 83°30'W.	1	-1.60	32.45	26.12
		10	-1.60	32.54	26.21
		25	-1.47	32.54	26.20
		50	-1.81	33.21	26.75
June 18	63°47'N. 83°25'W.	1	-1.33	30.91	24.88
		10	-1.20	32.50	26.15
		25	-1.60	32.72	26.34
		50	-1.78	33.08	26.64

stations are in the vicinity of South Bay, immediately south of Coral Harbour. The marked similarity in temperatures, salinities and densities from the surface to 50 m., up to the middle of June, is quite plain and leaves no doubt that there is vertical exchange during the winter. Comparison of the density values at 50 m. with those at 100 and 200 m. in summer shows there is no reason to suppose that the vertical exchange fails to reach the bottom of Hudson Bay. The reduction in salinity and very slight rise in temperature at the surface on June 18 indicates that melting of the ice had begun to take effect by that time.

#### FJORDS AND INLETS

It is characteristic of the typical fjord, with its shallow threshold at the mouth and deep water inside, that the water below the level of the threshold is more or less cut off from the circulation of the water outside and therefore loses heat; the result is that the deeper water inside the fjord is considerably colder, depth for depth, than the water outside the fjord. This is the characteristic which distinguishes the so-called "Arctic" fjords of West Greenland, with thresholds, from the "Atlantic" fjords, without thresholds, in which there is free interchange between the fjord water and the main current water outside. Sometimes the deep fjord water is so far removed from contact with the coastal water, and for such long periods of time, that it becomes stagnant and devoid of aerobic life, as in certain fjords in Norway (Strøm, 1939), British Columbia (Pickard, 1953a) and one fjord in northern Foxe Basin (Grainger, personal communication).

The *Calanus* expeditions of 1949-54 worked in several inlets, some of which are of interest for this and other reasons. A typical, though small, example of the threshold fjord with cold deep water is Victoria Bay on the northeast coast of Frobisher Bay, a small inlet at the mouth of the Countess of Warwick Sound, which appears to have been Martin Frobisher's main base in the 1570's. Victoria Bay is 100 fathoms (183 m.) deep and has a threshold of about 30 fathoms (55 m.). The Countess of Warwick Sound is nowhere much deeper than 55 m. and has a shallower region along its line of contact with Frobisher Bay itself, so that the effective depth of the threshold into Victoria Bay is less than this, probably (according to sounding runs made from the open water) about 20 fathoms (37 m.). Owing to the peculiar bathymetry of Frobisher Bay, depths similar to that of Victoria Bay do not occur within several miles of the mouth of the Countess of Warwick Sound; the closest are towards Station 324 to the west and 315 to the south. Temperatures and salinities for these two stations are given here in Table V, compared with those from Victoria Bay (Station 329).

The differences between the fjord water and the outside water are of course not so striking as in an area such as Ameralik Fjord in West Greenland (Dunbar, 1951), where the outside water is a great deal warmer than it is in Frobisher Bay. Nevertheless, the situation is the same in all important aspects. The temperatures in the upper layers down to the 50-m. level are higher than at the stations in Frobisher Bay, which is probably the result of vertical circulation set up by westerly winds blowing into the inlet; below this layer, from 100 m. down, the water is colder than outside, which is the normal fjord effect described above.

TABLE V

Station: Date:	315 Aug. 8		324 Aug. 13		329 Aug. 21	
Depth	Temp.	Salinity	Temp.	Salinity	Temp.	Salinity
m.	°C.	‰	°C.	‰	°C.	‰
0	1.40	31.44	3.40	31.23	2.40	31.52
10	-0.10	32.31	1.84	31.76	1.33	32.20
25	-0.84	32.52	-0.13	31.85	1.15	32.16
50	-1.06	32.90	-0.96	32.16	0.52	32.27
100	-1.16	32.47	-1.16	32.49	-1.66	33.31
160	...	...	...	...	-1.74	33.52
200	-0.94	33.32	-1.38	32.69	...	...
300	...	...	-1.39	33.04	...	...

The bathythermograph slide (not published here) for Station 329 shows that the thermocline is deep, between 50 and 65 m. The high salinities of the 100- and 160-m. water are also an indication of the degree to which the sub-threshold water in Victoria Bay is cut off from the circulation of the deeper water outside.

In two other inlets visited, at depths shallower than 100 m., water temperatures at all levels are warmer than those outside the fjord, not colder as in the case of the upper 50 m. of Victoria Bay. These are Sugluk Inlet (Station 617, Fig. 31) and Adlorilik (Fig. 35). Sugluk is on the Quebec shore of Hudson Strait;

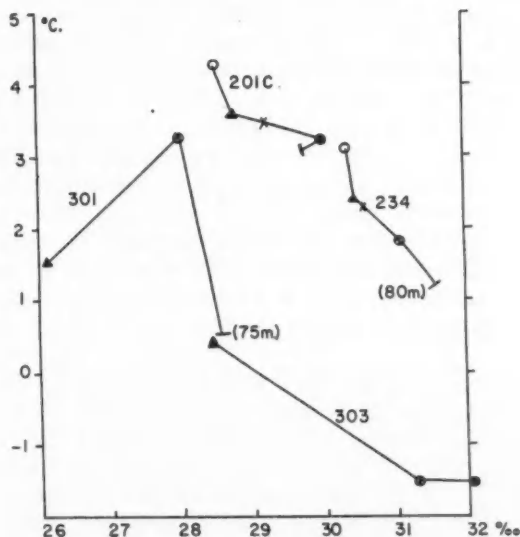


FIG. 35. Temperature-salinity correlation for stations in Adlorilik fjord (201C, August 29, 1950; 301, July 3, 1951) and outside the fjord in Ungava Bay (234, August 31, 1950; 303, July 4, 1951). Depth symbols as in Fig. 28.

Adlorilik is situated on the east side of Ungava Bay, 59°30'N., 65°26'W. It is called on the charts and topographic sheets "Abloviak", "Abluilluk" and other variants, none of which approaches the Eskimo pronunciation of the name. (See station list map, Dunbar and Grainger, 1952.)

The effect is more emphasized in the Adlorilik case than at Sugluk. Stations 201C (inside the fjord) and 234 (outside) were occupied on August 29 and 31, 1950; Stations 301 (inside) and 303 (outside) on July 3 and 4, 1951. In both pairs of stations the temperatures inside the fjord are quite considerably higher, and the salinities lower, than outside the fjord, depth for depth. The 1951 observations were made within two weeks, at the most, of the break-up of the ice in the fjord, so that the high temperatures at Station 301 at 50 and 75 m. must be the result of the retention of heat within the fjord throughout the winter. The 50-m. temperature in fact was the same on July 3, 1951, as on August 29 of the previous summer.

The sill depth at the mouth of Adlorilik is only about 22 to 25 m., so that the degree of isolation of the fjord water is considerable. A "hole" just inside the sill was sounded at 95 fathoms (174 m.); this appeared to be a deep pocket within an otherwise much shallower inlet, and no station was made in it. With this exception, the fjord is less than 100 m. deep.

The high temperatures and remarkably low salinities in Adlorilik, as compared with stations immediately outside the fjord, would suggest that down to 80 m. the only water in the fjord is water from the upper few metres of Ungava Bay, and that there is a constant or intermittent "flushing out" of the water, at least down to the depths measured; a phenomenon which must for the present remain unexplained. The prevailing northwesterly winds, the tidal current in a fjord of the long, narrow shape of Adlorilik, and the influx of water from the river at its head probably all play a part in the mechanism. The low salinity, which even at 80 m. is less than the surface salinity in late August in the body of Ungava Bay, is no doubt due to the freshwater influx. The derivation of the water of the fjord, or the great part of it, from the surface water of the bay outside, is further indicated by the nature of the plankton in the fjord, which will be dealt with in a later paper. There is a marked scarcity of Calanoid copepods and of copepods in general, and an abundance of Medusae at greater than normal depth.

The last inlet to be discussed here is a somewhat special case. Lake Ogac, meaning "Cod Lake", lies at the head of Ney Harbour, an inlet on the southwest shore of Frobisher Bay (Stations 312 and 312A, Grainger, 1954). At spring high tides there is some influx of salt water into the lake, in amounts at present unknown; for the rest of the time there is a current of overlying fresh water running into Ney Harbour, the outflowing stream being about 240 feet long. This outflow is of considerable volume, the stream being fast-flowing, about 90 feet wide on the average, and some 2 to 3 feet deep. The lake itself is quite small, in the shape of an "L" in which the longer arm is about a mile long and the shorter about  $\frac{1}{2}$  mile. There are three small basins in the lake, separated by shallower water, of which the central one is a little over 60 m. deep. The inner basin was



not sounded but is probably shallower, and the outer basin is about 20 m. deep. In the central basin there are three quite distinct layers of water: an overlying, very shallow fresh water layer derived from the inflowing drainage at the head of the lake, a layer of salt water of fairly low salinity, and a bottom layer of stagnant water rich in hydrogen sulphide and devoid of dissolved oxygen. The transition between the two lower layers appears to be gradual. There is no stagnant layer in the outer basin, which is small. Table VI gives temperatures, salinities and dissolved oxygen concentrations for two stations in the lake (312 in the central basin, 312A in the outer basin), and one station (313) in Ney Harbour.

TABLE VI. Ogac Lake and Ney Harbour; temperature, salinity and dissolved oxygen concentration.

Depth	Station: 312			312A			313		
	Date: August 4, 1951			August 4, 1951			August 5, 1951		
	Temp.	Salinity	Oxygen	Temp.	Salinity	Oxygen	Temp.	Salinity	Oxygen
m.	°C.	‰	cc./l.	°C.	‰	cc./l.	°C.	‰	cc./l.
0	7.40	0.00	7.35	7.70	0.00	8.30	4.40	28.00	8.64
10	7.31	22.32	7.54	6.40	26.99	7.09	1.21	31.83	8.17
18	...	...	...	3.88	27.47	4.11	...	...	...
25	8.12	26.10	2.01				0.03	32.35	6.89
50	4.50	26.95	0.00				-0.39	32.56	7.55
100							-0.93	32.62	6.33
160							-1.25	32.94	5.07

Lake Ogac can be considered as the extreme case of the fjord condition, with threshold so high that salt water can enter only in small quantity and intermittently, and with the "fjord" itself so small that there is very limited mixing between the overlying land-drainage water and the salt water below. The anaerobic layer at the bottom is also an extreme fjord characteristic. The salt water is heated by solar radiation to temperatures quite extraordinarily high for the geographical area, and it is insulated against heat loss by ice and snow in winter. The lake contains an unusual animal population including an isolated group of Atlantic cod (*Gadus callarias*). A thorough study of the lake is in progress in the field.

#### CONCLUSION

No lengthy discussion of the results, presented here somewhat tersely, is necessary. Emphasis should, however, be laid on one point, namely that much of the hydrodynamic pattern in the region under study is dominated and determined by the tides, and that the basic studies from which understanding of the tides would come have not yet been made. The behaviour of water under extreme tidal forces in these narrow seas can only be guessed at. The undulating profiles found in Ungava Bay, the behaviour of the currents in Frobisher Bay, the setting up of negative stabilities (presumably for quite limited periods), the fate of Atlantic water entering Frobisher Bay, and certain of the special conditions found in small fjords—all these appear to be determined, to a greater or lesser extent, by tidal forces. Since these phenomena are of great practical interest both in

the physical and biological sciences, it is fitting to close this paper with a plea for intensive study of the tides of this eastern Arctic area in particular, and of tidal behaviour in contained waters in general.

#### ACKNOWLEDGMENTS

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# Limnological Studies of Heming Lake, Manitoba, and Two Adjacent Lakes<sup>1</sup>

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## ABSTRACT

Heming, Home and Wapun Lakes are small, eutrophic lakes on the Precambrian Shield. They are at the headwaters of the Nelson River in northern Manitoba at approximately 55° N. longitude, 101° W. latitude. The lakes are each about one square mile in area and are all under 30 feet in depth. For four years physical and chemical studies have been conducted as part of the *Triaenophorus* investigation. During six months of the year the lake is ice-covered. No summer thermal or oxygen stratification is evident. Oxygen concentrations remain at a high level throughout the year. Summer water temperatures follow very closely changes in air temperature. The pH remains close to neutrality and the dissolved mineral content is about 60 p.p.m. The mineral content of these three soft water lakes is similar. Flora and fauna identified from Heming Lake include 41 genera of phytoplankton, 35 species of zooplankton, 17 genera of bottom organisms, 13 species of fish and 9 species of fish parasites.

## INTRODUCTION

In 1945 the Fisheries Research Board of Canada began an experiment at Heming Lake, Manitoba, to reduce the pike, *Esox lucius*, population in hope of improving the quality of whitefish, *Coregonus clupeaformis*, which was affected by the presence of cysts of the pseudophyllidean cestode, *Triaenophorus crassus* in the flesh. *T. crassus* in one of its immature stages is very common in the flesh of whitefishes in some Canadian lakes. The life history of this parasite has been fully described by Miller (1952).

In 1950 the program at Heming Lake was broadened to include fundamental studies on the life history of the parasite because it had become evident that any control measure would require a period of extensive research. The pike exploitation study has been continued in the hope of finding a more economical and efficient method of exploiting fish populations than those formerly used.

As part of the study, limnological data were collected to determine any relationships that might exist between the physical and chemical characteristics of the lake and the various stages in the life history of the parasite. Since the life history of the parasite is dependent on at least two fish as hosts, particular attention was given to determining the factors which govern the production and survival of these fish and of the other species of fish with which they interact. Those factors considered include the following: geology of the surrounding country, morphometry of the lake, temperature of the water and air temperature of the surrounding country, oxygen content, hydrogen-ion concentration, mineral

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content, transparency of the water, abundance of phyto- and zooplankton, and bottom fauna.

This is the first in a series of papers concerning the investigations into the *Triaenophorus* problem at Heming Lake. Particular attention is given here to a description of the physico-chemical properties and the fauna of the lake. Somewhat less detailed limnological records are presented for Wapun and Home Lakes, which are connected to Heming Lake. These lakes have different fish populations than Heming, differ greatly with regard to the parasite problem, yet are comparable in size and shape. This rather unusual situation may assist in better understanding the problem in Heming Lake.

#### PHYSIOGRAPHY AND MORPHOMETRY

##### LOCATION AND DRAINAGE SYSTEM

Heming, Wapun and Home Lakes (Fig.1) are situated in the province of Manitoba, Canada, in latitude  $54^{\circ}53'$  N.,  $101^{\circ}7'$  W. longitude, 18 miles south of Sherridon. The lakes lie in the headwaters of the Grass River which flows into the Nelson River at Split Lake, and are approximately 1,100 feet (360 m.) above sea level.

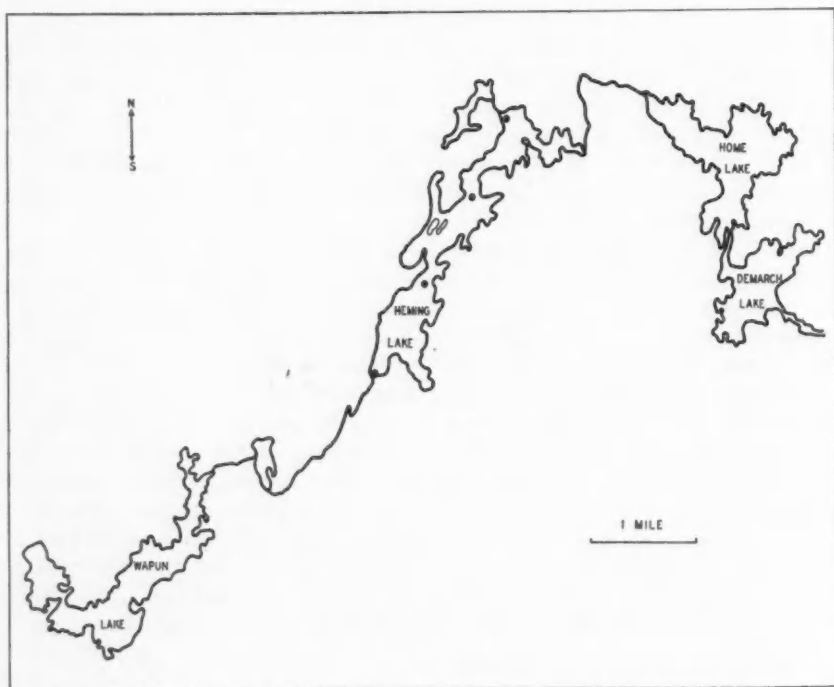


FIG. 1. Map of Heming Lake and adjacent lakes.

Wapun Lake, in the south, drains into Heming Lake through a small lake which is practically blocked at its outlet by a beaver dam, and then through a narrow, deep creek. This creek flows in a meandering course through muskeg, and is about 5 feet (1.6 m.) in width and 12 feet (4 m.) in depth where it nears the lake.

Heming Lake has a second, main tributary stream which flows into the northwest corner. It is only about  $\frac{1}{4}$  mile (0.4 km.) in length but drains a chain of small lakes into Heming Lake. A beaver dam 5 feet (1.6 m.) high, located where the creek begins, prevents fish from moving out of Heming Lake. There are a few other small creeks which arise in muskeg and drain into Heming Lake.

The outlet at the northeast corner, which drains Heming Lake into Home Lake about two miles distant, is 35 feet (11 m.) in width where it leaves Heming Lake. There are four rapids between Heming Lake and Home Lake with quieter, wider expanses of river between.

#### CLIMATE

The climate in the area may be considered northern continental, as the winters are long and cold, the summers short but warm and the annual precipitation is low.

The mean annual air temperature of the region is about  $-1.1^{\circ}\text{C}$ . ( $+30^{\circ}\text{F}$ .). Some figures from Thomas (1953) on mean temperature are: January,  $-23^{\circ}\text{C}$ . ( $-10^{\circ}\text{F}$ .); April,  $-1.1^{\circ}\text{C}$ . ( $+30^{\circ}\text{F}$ .); July,  $+15.6^{\circ}\text{C}$ . ( $+60^{\circ}\text{F}$ .); and October,  $+1.7^{\circ}\text{C}$ . ( $+35^{\circ}\text{F}$ .). Temperatures are recorded continuously during the summer months at Heming Lake and temperatures over  $32^{\circ}\text{C}$ . ( $90^{\circ}\text{F}$ .) are common in July. There are about 2,000 hours of bright sunshine annually which is higher than in the Great Lakes region where approximately 1,800 hours are recorded annually.

The precipitation is relatively low in the area, the mean annual being estimated between 15–20 inches (38–51 cm.). There are 10–15 inches (25–38 cm.) of rain and 40–60 inches (102–152 cm.) of snow per year.

Mean wind speeds during the year in the vicinity of Heming Lake are about 10 m.p.h. (1.6 km. per hr.). Winds from the northwest predominate during the winter. In the summer months while the wind direction is quite variable, winds from the northeast and southeast are the most common.

The severity of the winter is reflected in the length of time that the lake is covered by ice. Freeze-up usually occurs early in November and the lake remains frozen until mid-May. The depth of ice ranges from 13 inches to 3 feet, depending on the amount of snow cover.

#### GEOLOGY

The consolidated rocks in the Heming Lake area are Precambrian in age. The oldest rocks consist of metamorphosed basic volcanic rocks of Amisk age. These formations are represented in the immediate vicinity of Heming Lake by only a few outcrops west of the lake and one outcrop about a mile southwest. They are intruded by three types of granitic rocks which outcrop around Home and Wapun Lakes as well. These granites are all related and were intruded

during one period of orogeny but are of slightly different ages according to McGlynn (1955).

The unconsolidated material in the Heming Lake area is of quaternary age. The whole area has been glaciated and the glacial deposits consist of fine-grained sand, silty sand, and gravels. Glacial boulders are scattered about throughout the area. In the Heming Lake area glacial erosion predominates over deposition.

#### SIZE, SHORELINE, AND DEPTH

A comparison of the area, length of shoreline, and shoreline development of the three lakes is given in Table I. Heming Lake is the largest of the three lakes

TABLE I. Comparison of size, shoreline and depth of Heming, Wapun and Home Lakes.

Lake	Area	Max. depth		Length of shoreline	Shoreline development
		<i>feet</i>	<i>m.</i>		
Heming	640	18	5.5	12.8	3.6
Wapun	610	28	8.5	11.2	3.25
Home	448	12	3.7	8.3	2.6

considered, in total acreage, and length of shoreline. It has a calculated mean depth of 9.5 feet (2.9 m.) with a maximum depth of 18 feet (5.5 m.) which is greater than that of Home Lake 12 feet (3.7 m.), but considerably shallower than Wapun with a maximum depth of 28 feet (8.5 m.).

The relative volumes of water in Heming Lake in different depth strata have been calculated and are shown in Table II.

TABLE II. Percentage area of depth zones and percentage volume of strata of Heming Lake.

Depth zone	Percentage area of zone	Percentage volume of strata
<i>feet</i>	<i>%</i>	<i>%</i>
0-3	19.0	28.3
3-6	14.6	23.2
6-9	12.7	18.9
9-12	11.3	15.1
12-15	17.5	10.5
15-18	24.9	4.0

The total volume of the lake was estimated to be  $9.8 \times 10^6$  cubic yards ( $6.5 \times 10^6$  cu. m.).

The three lakes have many bays, about 6 feet (2 m.) deep, with muskeg shores and muck bottoms. There is usually a fringe of emergent and considerable submerged vegetation present. The remainder of the shoreline is composed of rock and sand.

#### PHYSICAL AND CHEMICAL ENVIRONMENTS

##### WATER TEMPERATURE

Water temperatures have been taken at Heming Lake each year since 1952 and the data are recorded in the Appendix. Most of the observations were taken



in the summer months; however, some observations were taken during the winter of 1953-54 and in February 1957. Temperature observations were made with a "maximum-minimum" thermometer when either plankton or water samples were taken.

A fairly general seasonal trend of temperature changes is repeated each year (Fig. 2). After break-up of the ice cover in the spring the water in the lake warms till the maximum summer temperature is reached in late July and early August. If wind action is strong enough, the warming is spread rapidly and only a slight temperature gradient exists from the surface to the bottom. In periods of calm sunny weather the surface layers of the lake may become considerably warmer than the deeper layers. However no permanent thermal stratification has

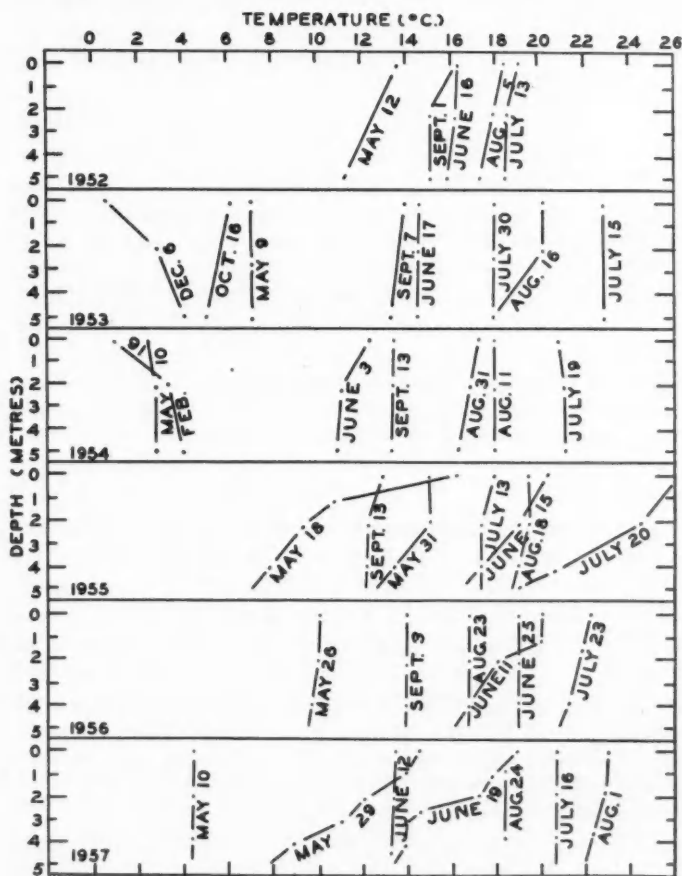


FIG. 2. Temperature-depth relationships in Heming Lake for the years 1952-57.

been observed in the lake. The water temperature in Heming Lake at any time in the summer period is strongly influenced by the existing climatic conditions. Lower air temperatures will temporarily reduce the water temperature just as an abnormally hot period will produce high water temperatures. Thus the temperature records for July 13, 1955 are lower than those of a month earlier while the summer maximum temperatures occurred only a week later on July 20. This is undoubtedly due to the shallowness of the lake.

Calculated values for total heat budget and summer heat income are shown in Table III. Winter temperatures for 1953-54 (Appendix) were used in calcu-

TABLE III. Heat Budgets of Heming Lake

Year	Total heat budget	Summer heat income
	<i>cal./cm.<sup>2</sup></i>	<i>cal./cm.<sup>2</sup></i>
1952	5035	4425
1953	6345	5735
1954	6010	5400
1955	6500	5890
1956	6100	5490

lating the total heat budget for the five years. The values of the total heat budget for Heming Lake (5,000-6,500 cal./cm.<sup>2</sup>) are much lower than those for larger, deeper lakes (around 20,000 cal./cm.<sup>2</sup>—Rawson, 1950). The low heat budget of Heming Lake is an expression of the ease with which such a shallow lake warms up.

Temperature observations have also been made for Home and Wapun Lakes. Although the records are less complete than those for Heming Lake, a similar temperature pattern is indicated.

#### DISSOLVED OXYGEN

Dissolved oxygen was determined by the Miller method (DeLaporte, 1920). Titrations were done within an hour after the water samples were taken. The values obtained were corrected for altitude and percentage saturation values were calculated using Rawson's (1945) nomogram (see Appendix).

Heming Lake is a shallow body of water which can mix freely to all depths. This mixing tends to maintain the dissolved oxygen content of all waters near the saturation level. Thus during the summer months the absolute amount of dissolved oxygen in the lake is controlled by the water temperature.

Home and Wapun Lakes both are similar to Heming Lake in the amounts of dissolved oxygen in the water. They too have the dissolved oxygen content controlled by temperature in the summer months.

Under ice cover there is considerable oxygen depletion in the deep waters of Heming Lake. Values of 33-60% saturation at 15 feet (4.6 m.) were found in five samples taken from February 24 to May 7, 1954 and 60% saturation was observed at 12 feet (3.7 m.) in one sample taken February 24, 1957.

### HYDROGEN-ION CONCENTRATION

The pH was measured with a Hellige comparator. The determinations were made at the same time as those for oxygen.

The range of variation of pH for Heming Lake is 6.2 to 7.3 units. The great majority of the readings are very close to neutrality (between 6.8 and 7.2). (Appendix.) Lower values occasionally occur in both deep and shallow water.

There is no difference in the range of pH values observed for Home and Wapun Lakes from that found for Heming Lake. The majority of readings for both lakes lie between 6.9 and 7.1 units.

### TRANSPARENCY

The water is brownish in colour, a characteristic of lakes in muskeg regions. The light penetration based on Secchi disc observations, determined at comparable time, ranged from 3.5 to 7.5 feet (1.1–2.3 m.).

### MINERAL CONTENT

Water samples from Heming, Home and Wapun Lakes collected in August 1957 have been analyzed by the National Testing Laboratories Ltd., Winnipeg, Man. (Table IV). The amount of total solids present and the main mineral con-

TABLE IV. Analyses of water collected at Heming, Wapun and Home Lakes in August 1957. All figures except pH are in parts per million by weight.

Appearance	Heming Lake Yellow, with very slight organic suspension	Home Lake Yellow, with some organic suspension	Wapun Lake Yellow, with very slight organic suspension
pH	7.45	7.20	6.80
Total solids by evaporation	61.	67.	57.
Organic solids	32.	46.	32.
Nitrate nitrogen	0.08	0.03	0.05
Phosphate ( $\text{PO}_4$ )	0.001	0.005	0.035
Alkalinity (total as $\text{CaCO}_3$ )	18.5	16.	16.
Mineral analysis			
Calcium (Ca)	6.6	2.4	5.6
Magnesium (Mg)	0.5	2.4	1.2
Sodium (Na)	1.8	1.4	1.5
Carbonate ( $\text{CO}_3$ )	11.1	9.6	11.4
Sulphate ( $\text{SO}_4$ )	2.9	2.3	2.6
Chloride (Cl)	0.7	0.4	0.4
Total hardness	19.	21.	19.

stituents are essentially the same in the three lakes. The values for the total solids are near the average for lakes on the Precambrian Shield (Rawson, 1951).

There is some evidence of annual variation in total solid content as the samples from Heming Lake in the years 1954, 1955, 1956 and 1957 contained 68, 75, 81 and 61 ppm. total solids, respectively. One explanation of the annual difference is that the time of sampling was not the same in the years in question.

## PLANKTON

## ZOOPLANKTON

Quantitative zooplankton observations on Heming Lake were made at two open water stations in the deep part of the lake and at two shallow water stations close to the main inlets during the summer seasons from 1952 to 1956 and during the winter of 1953-54. These samples were taken with a 10-litre Juday trap. Samples in shallow water areas were taken in the spring of each year with a Wisconsin-type tow net of #20 bolting silk. Some collections from Home and Wapun Lakes were made during the summers of each of the five years.

Eleven species of cladocerans and 11 species of copepods have been recorded from the plankton of Heming Lake. In addition, at least four other species of cladocerans and five species of copepods have been observed in preliminary investigations of the littoral and marsh plankton.

A list of the crustacean plankton organisms from Heming Lake is given below. Specimens have been examined and their identification confirmed by Dr. H. C. Yeatman, University of North Carolina (species marked with an asterisk, \*) and by Dr. J. L. Price, University of Toronto (species marked by a dagger, †).

## (A) LIMNETIC FAUNA

## (1) CLADOCERA

- \**Bosmina longirostris* (O.F.M.)
- \**Ceriodaphnia reticulata* (Jurine)
- \**Chydorus sphaericus* (O.F.M.)
- \**Daphnia longispina* (O.F.M.)
- \**Daphnia pulex* (de Geer)
- \**Diaphanosoma brachyurum* (Lievin)
- \**Holopedium gibberum* Zaddach
- \**Leptodora kindti* (Focke)
- \**Pleuroxus denticulatus* Birge
- \**Polyphemus pediculus* (L.)

## (2) COPEPODA

- \*†*Cyclops bicuspidatus thomasi* Forbes
- \*†*Cyclops vernalis* Fischer
- \**Diaptomus minutus* Lillj.
- \**Diaptomus oregonensis* Lillj.
- \**Epischura lacustris* Forbes
- \**Epischura nevadensis* Lillj.
- \*†*Eucyclops prasinus* (Fischer)
- \**Ergasilis* sp.
- \**Mesocyclops edax* (Forbes)
- †*Mesocyclops leuckarti* (Claus)

## (B) ADDITIONAL FORMS FROM LITTORAL AREAS

## (1) CLADOCERA

- Acroperus harpae* Baird
- Ilyocryptus* sp.
- Latona setifera* (O.F.M.)

*Sida crystallina* (O.F.M.)  
*Simocephalus vetulus* (O.F.M.)

(2) COPEPODA

- †*Canthocampus* sp.
- †*Cyclops varicans* Sars
- †*Cyclops venustoides* Coker
- \*†*Eucyclops agilis* (Koch)
- †*Macrocyclus albidus* (Jurine)

The most abundant species of the plankton are the copepods, *Cyclops bicuspidatus*, *Diaptomus minutus* and the cladoceran, *Bosmina longirostris*. Other species which are present in smaller numbers are *Eucyclops prasinus*, *Diaptomus oregonensis*, *Daphnia* spp. and *Chydorus sphaericus*. During each summer, *Epischura nevadensis*, *Diaphanosoma brachyurum* and *Holopedium gibberum* may be quite common for short periods of time. In an unpublished report, I. G. Arnason states that the zooplankton of Heming Lake is among the most varied and abundant of 73 Manitoba lakes studied.

In the shallow bays, especially among submerged aquatic vegetation the fauna is quite different from the open water plankton. *Eucyclops prasinus* is more numerous than *Cyclops bicuspidatus* and *Eucyclops agilis* and *Cyclops vernalis* are more common here than in the main lake. The cladocerans outnumber the copepods both in numbers of individuals and in numbers of species. This is due to the large swarms of *Bosmina*, *Daphnia*, *Diaphanosoma* and occasionally *Polyphemus* which develop under favourable conditions. We have also collected from this habitat such forms as *Sida crystallina*, *Latona setifera*, *Simocephalus vetulus* and *Acroperus harpae* which are more correctly bottom or crawling forms rather than plankton.

A few preliminary samples from marsh pools on the flood plain of Heming Creek yielded a very different copepod fauna from that in the lake proper. *Cyclops varicans*, *Macrocyclus albidus*, *Eucyclops agilis* and *Mesocyclus leuckarti* seem to be the dominant forms. *Chydorus* and *Bosmina* are the most common cladocerans in this marshy area.

The plankton of Home and Wapun Lakes, in as far as the available data have been analyzed, appears quite similar to that of Heming Lake. All the major species found in Heming Lake have been recorded for each of these lakes.

#### PHYTOPLANKTON

A brief study of the phytoplankton of Heming Lake was undertaken in connection with zooplankton studies. In 1956 some of the phytoplankton obtained in the regular Juday trap series was examined to determine the species present. Samples were chosen from the collections taken during the latter part of June and early July and from collections made during early September. Forty-one genera of algae were identified by the junior author.

The following is a list of the genera identified from Heming Lake samples:—

## I. Division CYANOPHYTA

## MYXOPHYCEAE

## CHROOCOCCALES

*Coelosphaerium*, *Merismopedia*, *Microcystis*

## NOSTOCALES

*Anabaena*

## RIVULARIALES

*Gleotricha*

## II. Division CHLOROPHYTA

## CHLOROPHYCEAE

## VOLVOCALES

*Eudorina*, *Volvox*

## CHLOROCOCCALES

*Coelastrum*, *Dictyosphaerium*, *Dimorphococcus*, *Pediastrum*, *Scenedesmus*, *Selenastrum*, *Tetraedron*, *Westella*

## ZYGNEMATALES

*Arthrodesmus*, *Closterium*, *Cosmarium*, *Euastrum*, *Micrasterias*, *Netrium*, *Staurastrum*, *Xanthidium*

## III. Division CHRYSOPHYTA

## CHRYSOPHYCEAE

*Chrysosphaerella*, *Dinobryon*, *Mallomonas*, *Synura*

## BACILLARIOPHYCEAE

## CENTRALES

*Melosira*, *Stephanodiscus*

## PENNALES

*Asterionella*, *Amphora*, *Cymbella*, *Diatoma*, *Fragilaria*, *Gomphonema*, *Navicula*, *Stauronius*, *Surirella*, *Synedra*, *Tabellaria*

## IV. Division PYRRHOPHYTA

## DINOPHYCEAE

*Ceratium*

Diatoms, including *Melosira* sp., *Tabellaria* sp., and *Asterionella* sp., and blue-green algae, including *Anabaena* spp. were the predominant species in all samples. Among the green algae present, the most noticeable forms were several species of Chlorococcales and numerous species of Desmids. The desmid fauna of Heming Lake is composed of a large number of species. However, there are few individuals of any one species to be found in any one sample. Some species are recorded which are not generally considered truly planktonic. Notable among these are the relatively large and striking species of *Micrasterias* and *Euastrum*. The most common genus of desmids is *Staurastrum* with at least five species in Heming Lake.

The Chlorococcales, though never abundant, are a constant constituent of the summer plankton of Heming Lake. *Pediastrum*, *Tetraedron* and *Dictyosphaerium* are the most important genera of this group.

Members of the Chrysophyceae are seasonally important in the plankton. The two most prominent genera in this group are *Dinobryon* and *Synura*.

*Ceratium*, a dinoflagellate, is also a common member of the plankton at most times of year.

The phytoplankton of Home and Wapun Lakes is similar in composition to that of Heming Lake. Only a few samples have been examined, but all of the common forms in Heming Lake have been found in the other two. Blue-green algae seem to be slightly less abundant in Wapun Lake, at least in late summer.

Since they are primary producers in the economy of any lake, the phytoplankton algae have been considered indicators of the trophic type. Rawson (1956) emphasizes that the dominant species in a lake should be the ones which are used in assigning it any degree of productivity. In Heming Lake *Tabellaria*, *Melosira*, *Ceratium*, *Anabaena* and *Microcystis* are the dominant genera of phytoplankton during the summer months. These species indicate its eutrophic character. This is substantiated by the presence of secondary genera, *Stephanodiscus*, *Pediastrum* and *Volvox*. A third evidence of the phytoplankton productivity of Heming Lake is the frequent blooms of blue-green algae which occur each summer.

#### BOTTOM FAUNA

A preliminary investigation of the bottom fauna of Heming Lake was made in 1945 by Sprules (MS) to complement the study of the food of whitefish in the lake. This program was resumed in 1956 and bottom fauna samples were taken from Heming, Home and Wapun Lakes.

Eleven Ekman dredge and 50 Petersen dredge samples were taken from Heming Lake in 1956. Following is a list of the organisms found in those samples:—

##### ANNELIDA

OLIGOCHAETA (several genera)

##### MOLLUSCA

GASTROPODA (several genera)

##### PELECYPODA

*Sphaerium*, *Pisidium*, *Anodonta*

##### CRUSTACEA

*Hyaella*; *Cambarus* (in rocky stretches of shoreline)

##### INSECTA

###### EPHEMEROPTERA (Mayflies)

*Ameletus*, *Ephemerella*, *Hexagenia*, *Tricorythodes*

###### ODONATA (Dragonflies and Damselflies)

*Macromia*, *Anomalagrion*

###### MEGALOPTERA (Alderflies)

*Sialis*

###### TRICHOPTERA (Caddisflies)

*Astenophylax*, *Limnephilus*, *Molanna*, *Polycentropus*

###### DIPTERA (two-winged flies)

Culicidae: *Chaoborus*

Chironomidae

Ceratopogonidae

Tabanidae

Heming Lake may be divided at approximately the 9-foot (2.8-m.) level into two zones. Below this level the bottom is covered with a deep layer of dark brown ooze. Above this level there are several different types of bottom. Much of the lake has steep, boulder-strewn sides but there are also several shallow bays where the bottom is either sandy or, adjacent to muskegs, peaty. In the deeper part of the lake *Chaoborus*, *Chironomids* and *Sphaerium* are found. *Hexagenia* and *Hyallela* are the most abundant organisms in the shallower bottoms of the lake. However, these regions contain most of the other organisms present as well because they have a greater diversity of habitat types.

#### FISH AND FISH PARASITES

Thirteen species of fish have been found in Heming Lake, but not all were found in Home and Wapun Lakes. Those found in Heming Lake are:

Northern pike	<i>Esox lucius</i>
Yellow walleye	<i>Stizostedion vitreum vitreum</i>
Lake whitefish	<i>Coregonus clupeaformis</i>
Cisco or tullibee	<i>Leucichthys</i> sp.
Common white sucker	<i>Catostomus commersoni commersoni</i>
Yellow perch	<i>Perca flavescens</i>
Burbot	<i>Lota lota lacustris</i>
Spottail shiner	<i>Notropis hudsonius</i>
Johnny darter	<i>Etheostoma nigrum</i>
Eastern slimy sculpin	<i>Cottus cognatus gracilis</i>
Brook stickleback	<i>Eucalia inconstans</i>
Ninespine stickleback	<i>Pungitius pungitius</i>
Troutperch	<i>Percopsis omiscomaycus</i>

Wapun Lake is the largest and deepest of the three and appears well suited for the maintenance of a coregonine population, yet neither *Coregonus clupeaformis* nor *Leucichthys* is present. In Heming Lake, which is intermediate in size and depth among the three lakes, both species are present with the whitefish dominant. Home Lake has a small population of very large whitefish, but no cisco population.

The northern pike and the yellow walleye are present in all three lakes. The pike is dominant in Heming Lake while the yellow walleye is more abundant in Wapun and Home Lakes.

Yellow perch, white sucker and troutperch are common in all three lakes and are important items in the diet of the predacious fish.

Fingerling burbot are abundant in the three lakes but adults are only rarely found in the net catches.

Other species commonly found are the Johnny darter, the eastern slimy sculpin, the brook stickleback, the ninespine stickleback and the spottail shiner.

Members of the genus *Triaenophorus* appear to be the most common parasites in Heming Lake (Table V). The apparent reason is that suitable hosts necessary for the completion of the life cycle are abundant, whereas the necessary hosts for the other species listed may not be so abundant.



TABLE V. Cestodes found in 11 species of Heming Lake fish examined during 1953. Species marked by an asterisk were identified by Mr. Scott W. Little, Dept. of Zoology, University of Manitoba.

Species of cestode	Species of fish
<i>Triaenophorus crassus</i>	<i>Coregonus clupeaformis</i> <i>Leucichthys</i> sp. <i>Esox lucius</i>
<i>Triaenophorus nodulosus</i>	<i>Esox lucius</i> <i>Perca flavescens</i> <i>Cottus cognatus gracilis</i> <i>Lota lota lacustris</i>
<i>Triaenophorus stizostedionis</i>	<i>Stizostedion vitreum vitreum</i> <i>Percopsis omiscomaycus</i> <i>Cottus cognatus gracilis</i>
* <i>Proteocephalus singularis</i>	<i>Coregonus clupeaformis</i>
* <i>Proteocephalus pinguis</i>	<i>Esox lucius</i>
* <i>Proteocephalus luciopercae</i>	<i>Stizostedion vitreum vitreum</i>
* <i>Schistocephalus solidus</i>	<i>Cottus cognatus gracilis</i> <i>Eucalia inconstans</i>
* <i>Dibothriocephalus latus</i>	<i>Esox lucius</i> <i>Stizostedion vitreum vitreum</i>
* <i>Ligula intestinalis</i>	<i>Catostomus commersoni</i> <i>Notropis husdonius</i>

#### DISCUSSION

Heming, Home and Wapun Lakes are similar to many other small shallow lakes situated on the Precambrian Shield of Northern Canada. Extensive studies of lakes of this type have not been made because of the relative inaccessibility of the areas in which they are located and because their small size makes them unsuitable for commercial fishing operations.

Analysis of the effect of climatic, edaphic and morphometric factors on the productivity of lakes (Rawson, 1955) appears to indicate that the shallow small lakes of this region should be eutrophic if climatic and edaphic factors were favourable. Heming, Home and Wapun Lakes support relatively abundant populations of many species of plankton, bottom organisms and fish. Data on mineral content, dissolved oxygen and pH indicate an adequate physical environment for the organisms in the lakes. Therefore it would seem that in the three lakes of this study climatic factors, especially temperature, are most important in determining the degree of productivity that is attained.

Temperatures in these lakes may fluctuate widely over relatively short periods of time and along with other climatic conditions may possibly affect the size and survival of a year class of fish as suggested by Miller (1956) for one Alberta lake.

These three lakes provide a useful field situation for the study of the inter-relationships involved in the *Trienophorus*-coregonine-pike cycle. Heming Lake has two species of coregonines heavily infected with *Trienophorus crassus*, Home Lake has a small population of non-infected whitefish only, and Wapun Lake has no coregonines. The preliminary investigations discussed in this paper indicate that the three lakes are basically similar. The key to the different situations found here should reveal some reason for the difference in host-parasite relationships in the three lakes.

#### SUMMARY

1. Heming, Home, and Wapun Lakes are small, shallow, eutrophic lakes on the northern part of the Nelson River drainage lying in glaciated Precambrian rock. Heming Lake, which was the most intensively studied, has a surface area of one square mile and a mean depth of about 10 feet (3.0 m.).

2. No summer thermal stratification was present in any of the three lakes. Temperature differences between surface and bottom seldom exceeded four Fahrenheit degrees. Summer water temperatures of Heming Lake during the five years of the study followed closely the mean air temperature.

3. Dissolved oxygen at all depths in the three lakes approached total saturation throughout the summer. Some oxygen depletion occurs at the bottom of Heming Lake during the winter.

4. The total dissolved solid content of the water in the three lakes is between 57 to 61 ppm.

5. There is a rich and varied zooplankton fauna. *Diaptomus minutus*, *Cyclops bicuspidatus*, and *Bosmina longirostris* are the most common limnetic entomostracans. The littoral micro-fauna contains several species of cladocerans and copepods not found in open water.

6. The phytoplankton of Heming Lake contains many species. The most important groups are the diatoms, desmids, chlorococcales and the blue-green algae in the early summer.

7. A preliminary survey of the bottom fauna indicates that *Chaoborus*, *Chironomus* and several species of mayflies are the most numerous forms.

8. A total of thirteen species of fish are recorded from the three lakes. Heming Lake which contains all of these has two species of coregonid fish. Wapun Lake has no coregonines and Home Lake only one coregonine, the whitefish. Pike, yellow walleye, perch, white sucker, and burbot are present in all three lakes.

9. A preliminary list of fish parasites includes nine species of cestodes from eleven species of fish. Three species of the genus *Trienophorus* occurred in eight species of fish.

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## APPENDIX

Some temperature, oxygen, oxygen saturation, and pH values for Heming Lake for the years 1952-57.

Date	Depth	Temp.	Oxygen	Oxygen sat'n	pH	Date	Depth	Temp.	Oxygen	Oxygen sat'n	pH
	feet	°C.	cc./l.	%			feet	°C.	cc./l.	%	
<b>1952</b>						<b>1954</b>					
May 12	0	13.3	7.25	98	7.2	Feb. 16	0	0.6	10.3	100	...
	15	11.1	7.05	91	7.0		6	3.33	9.2	97	...
June 16	0	16.1	6.6	95	...		15	4.0	8.3	90	...
	6	16.1	...	...	...	Feb. 24	0	0.6	8.7	85	...
	15	15.6	...	...	...		6	2.8	8.0	84	...
July 13	0	18.9	6.8	100	7.1		15	4.0	5.25	58	...
	6	18.3	...	...	...	Mar. 2	0	0.3	8.9	87	...
	15	18.3	6.7	98	7.0		6	2.2	8.5	87	...
Aug. 5	0	18.3	6.8	102	7.1		15	4.0	3.7	40	...
	6	17.8	...	...	...	April 1	0	0.6	9.0	87	...
	15	17.2	6.5	95	7.1		6	2.2	8.0	80	...
Sept. 1	0	16.1	...	...	...		15	4.0	3.5	37	...
	6	15.0	...	...	...	May 5	0	0.6	9.35	90	...
	15	15.0	...	...	...		6	2.2	...	...	...
<b>1953</b>							15	3.3	3.05	33	...
May 9	0	7.0	7.55	87	6.8	May 10	0	2.2	...	...	...
	9	7.0	7.45	81	6.8		6	2.8	...	...	...
June 1	0	13.3	7.35	99	7.1		15	2.8	...	...	...
	6	12.8	...	...	...	May 21	0	5.6	...	...	...
	15	12.2	7.25	95	7.0		6	5.6	...	...	...
June 17	0	14.4	6.5	90	7.0		15	5.6	...	...	...
	6	14.4	...	...	...	June 3	0	12.2	...	...	...
	15	14.4	6.4	88	7.0		6	11.1	...	...	...
July 5	0	17.8	6.8	100	7.0		15	10.8	...	...	...
	15	17.2	6.7	97	7.0	July 8	0	18.8	6.0	92	7.0
July 15	0	22.7	...	...	...		6	18.8	5.9	90	6.7
	15	22.7	...	...	...		15	18.8	6.0	92	7.1
July 30	0	17.8	6.6	98	7.1	July 19	0	20.6	6.0	93	7.1
	6	17.8	...	...	...		6	21.0	6.0	95	7.1
	15	17.8	...	...	...		15	21.0	5.35	85	6.8
Aug. 16	0	20.0	...	...	...	Aug. 11	0	17.8	6.6	97	6.9
	6	20.0	...	...	...		6	17.8	6.85	100	6.9
	15	17.8	...	...	...		15	17.8	6.4	95	6.9
Aug. 24	0	22.2	6.6	108	7.2	Aug. 31	0	17.2	6.5	92	7.1
	6	22.2	...	...	...		6	16.7	6.4	93	6.5
	15	20.0	6.3	103	7.0		15	16.1	6.1	87	6.5
Sept. 7	0	13.9	6.1	85	7.1	Sept. 13	0	13.3	6.7	92	6.9
	15	13.3	6.1	83	7.1		6	13.3	6.85	95	6.9
Oct. 16	0	6.1	9.35	106	...		15	13.3	6.5	87	6.9
	15	5.0	9.55	106	...						
Dec. 6	0	0.6	...	...	...						
	6	2.8	...	...	...						
	15	4.0	...	...	...						

## APPENDIX—Continued

Date	Depth	Temp.	Oxygen	Oxygen sat'n	pH	Date	Depth	Temp.	Oxygen	Oxygen sat'n	pH
	feet	°C.	cc./l.	%			feet	°C.	cc./l.	%	
<b>1955</b>						<b>1957</b>					
May 18	0	16.1	...	...	...	May 10	0	4.4	...	...	...
	3	10.6	...	...	...		6	4.4	...	...	...
	6	9.4	...	...	...		12	4.4	...	...	...
May 31	12	7.7	...	...	...	May 17	0	12.2	7.7	100	6.9
	0	15.0	6.7	95	...		6	12.2	...	...	...
	6	15.0	6.5	92	...		12	12.2	7.55	98	6.7
June 15	12	13.3	6.6	90	...	May 29	0	14.4	7.45	102	7.1
	0	20.0	...	...	...		3	13.9	...	...	...
	6	18.9	...	...	...		6	12.0	...	...	...
June 22	12	17.2	...	...	...	June 12	9	11.1	...	...	...
	0	18.9	6.3	92	6.6		12	8.9	7.75	95	6.7
	6	18.3	6.3	94	6.7		0	13.3	7.55	100	7.2
July 13	12	17.8	6.2	92	6.8	June 19	6	13.3	...	...	...
	0	17.8	6.4	96	6.8		12	13.3	7.05	95	6.9
	6	17.2	...	...	...		0	18.3	6.4	97	7.0
July 20	12	17.2	6.2	92	6.8	July 3	3	17.8	...	...	...
	0	26.1	...	...	...		6	17.2	...	...	...
	6	24.0	...	...	...		9	13.9	...	...	...
July 23	12	20.6	...	...	...	July 16	12	13.9	6.0	83	6.7
	0	21.1	5.65	90	6.8		0	19.4	5.7	87	6.7
	6	21.1	...	...	...		6	19.4	...	...	...
Aug. 18	12	20.0	5.9	93	6.8	Aug. 1	12	18.9	5.45	83	6.9
	0	19.4	6.6	100	7.1		0	20.6	5.7	90	6.9
	6	19.4	...	...	...		6	20.6	...	...	...
Sept. 6	12	18.9	6.7	102	7.0	Aug. 23	12	20.6	5.55	87	7.0
	0	15.6	...	...	...		0	22.8	5.45	90	7.0
	6	14.4	...	...	...		6	22.8	...	...	...
Sept. 13	12	13.9	...	...	...		12	22.2	5.55	92	6.9
	0	12.8	7.15	96	7.0		0	18.3	6.75	100	7.0
	6	12.2	7.25	96	6.8		6	18.3	...	...	...
	12	12.2	7.05	93	6.8		12	18.3	6.6	98	7.0
<b>1956</b>											
May 28	0	10.0	6.0	78	6.7						
	6	10.0	5.8	74	6.7						
	12	9.7	5.9	74	6.4						
June 7	0	16.1	...	...	...						
	6	15.6	...	...	...						
	12	15.0	...	...	...						
June 11	0	20.0	6.2	97	6.8						
	3	20.0	...	...	...						
	6	17.8	...	...	...						
June 25	12	16.7	5.65	85	6.9						
	0	18.9	5.8	89	7.2						
	6	18.9	...	...	...						
July 9	12	18.9	5.65	85	7.1						
	0	20.0	5.9	92	7.1						
	6	18.9	...	...	...						
July 23	12	17.8	5.9	87	7.3						
	0	22.2	6.1	100	7.0						
	6	21.7	5.9	97	7.0						
Aug. 7	12	21.1	5.9	95	7.0						
	0	20.6	5.8	92	7.0						
	6	20.0	...	...	...						
Aug. 23	12	20.0	5.65	88	...						
	0	16.7	6.0	90	7.1						
	6	16.7	6.0	90	7.1						
Sept. 3	12	16.7	5.9	88	7.1						
	0	13.9	6.7	92	7.1						
	6	13.9	6.7	92	7.1						
	12	13.9	6.7	92	7.1						

# Some Aspects of Growth and Reproduction of the Bearded Seal, *Erignathus barbatus* (Erxleben)<sup>1</sup>

"CALANUS" SERIES No. 13

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## ABSTRACT

This preliminary study is based on material from 113 specimens from the eastern Canadian Arctic. Animals may be aged from the claws up to 9 to 16 years. The male matures at 7 and the female at 6 years. The pup is produced around May 1 and the males are probably in full rut in mid-May. Females which have produced a pup forego ovulation until after the male rut, thus establishing a two-year cycle of pup production. The embryo implants during a 1½-month period around early August, after 2½ months of delay in development. The animal grows from 120 cm. in nose-tail length at birth to about 235 cm. The female increases her length by about 33% in the first year and reaches about 91% of her final length at puberty, at 6 years; these figures are somewhat larger than expected from the growth patterns of other Pinnipedia.

## INTRODUCTION

THE BEARDED SEAL, *Erignathus barbatus* (Erxleben), is rather sparsely distributed in the eastern Canadian Arctic. It is utilized as food by seal-hunting Eskimos, and its thick skin is particularly valuable for use in dog-team traces, harpoon lines, footgear, and other native products which require strong, durable hide. Material from 113 specimens has been collected from 1947 to 1956 by the M.V. *Calanus* and associated parties, in Ungava Bay, southwest and northern Baffin Island, northern Foxe Basin, and northern Hudson Bay.

Application of the tooth-aging technique has elucidated the patterns of growth and reproduction in several species of Pinnipedia. A number of workers, utilizing the recent findings, are engaged in comparative studies of this group. For example, some of the relationships between growth and sexuality of Pinnipedia have been published by Laws (1956a). The bearded seal has been the subject of two important papers by Russian workers (Chapsky, 1938; Sleptsov, 1943), but the animal has not been studied in detail in the American Arctic. The present study, though preliminary, may be of value, since it is the first to utilize an accurate aging method.

The method of aging seals from sections of their canine teeth (Laws, 1953; Fisher and Mackenzie, 1954; McLaren, in press) was found to be not applicable to the bearded seal, whose teeth are degenerate and often missing. Aging harp seals, *Phoca groenlandica*, from their claws was first practised by Plekhanov (1933) and has been fully described for the ringed seal, *Phoca hispida*, by McLaren (in press). The same method offers a valid indication of age of the

<sup>1</sup>Received for publication May 27, 1957.

bearded seal. A study of 62 claws, collected since 1954, indicates that a light band is laid down in the spring and summer, and that generally a ridge is formed during the period of moult in the spring. Wearing at the tip eliminates the first year's growth after 9 to 16 years of life.

#### GROWTH AND AGE

The size at birth of the bearded seal has not been well established. The pup is rarely taken, and most lengths of young bearded seals in the literature are from animals which have achieved independence of their parent. Sleptsov (1943), working with a large number of specimens, considered the birth size to be about 120 cm., from extrapolation of known summer lengths. A new-born pup observed east of Belle Isle on April 19, 1952, was 47 inches (119.5 cm.) from tip of nose to end of tail (D. E. Sergeant, personal communication). A full-term foetus was taken in Cumberland Sound on April 28 by Kumlien (1879) and was 4 feet 7 inches in extreme length. The hindflippers were 12 inches (30 cm.) long, and the tail of an animal of this length would be about 3 inches or 7.6 cm. (from regression line of 13 older animals); this suggests a nose-tail length of about 3 feet 10 inches (117 cm.). Another advanced foetus from Greenland measured 112 cm. from nose to end of tail on March 17 (Vibe, 1950). The youngest animals taken in the present study, from June 17 to July 4, ranged from 117 cm. to 147.5 cm. in length.

Figure 1 outlines the sizes of seals of known ages. Seals from all areas are

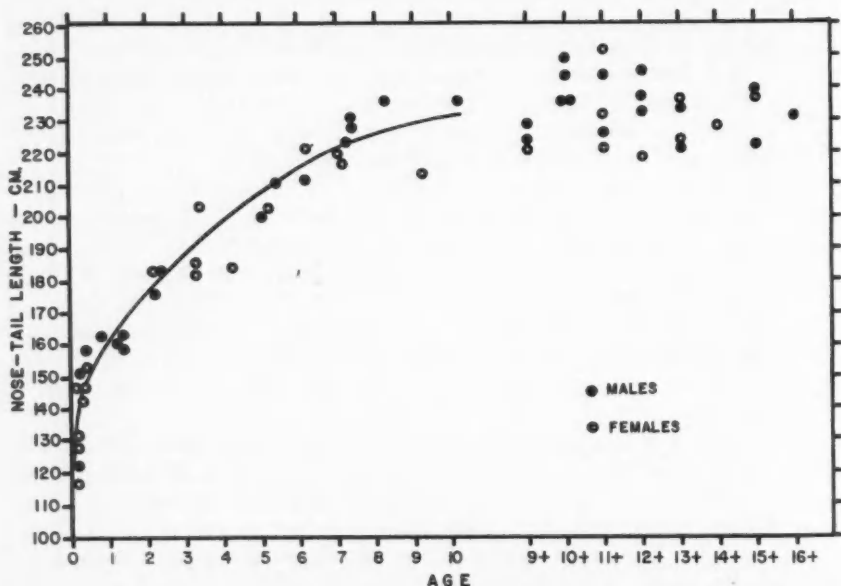


FIG. 1. Relation between nose-tail length and age in years of the bearded seal. Animals with indicated ages from 9+ to 16+ years could not be fully aged, due to the loss through wearing of the first year's growth band on the claws.

included together, since there is no evidence for geographical variation in size. Older seals, whose claws did not permit determination of full age, appear to average about 235 cm. in length. Some authors suggest that the male bearded seal averages somewhat larger than the female, but there is only slight evidence of this in the figure.

#### REPRODUCTION

##### AGES AT SEXUAL MATURITY

Thienemann (cited by Mohr, 1952) considered bearded seals of four years to be fully grown, and Sleptsov (1943) deduced from size-groupings that both males and females mature after their third year—a few females were supposed to mature at a younger age. Size-groupings of Pinnipedia have been found to be of little value in indicating age, in the light of recent studies in which the animals have been aged from their teeth.

The testis of a five-year-old seal on April 3 was small and inactive, although a few spermatids were detected. A larger testis was secured from a seal which was six years and two months old on July 2. This testis was quite active, with enlarged epididymis and testis tubules, but there was no evidence of spermia or their degenerate remains, as found in older testes at this season; the specimen probably represents the limited sexual activity of adolescence. An eighth-year testis on August 9 contained large numbers of spermatids, and the associated epididymis was filled with colloidal matter, degenerate cell remains, and spermatogenic cells; the condition resembled that of older males at this season. Another testis of the same age on August 29 was similarly active. Table I summarizes the

TABLE I. Spermatogenic activity, length and width of testes in millimetres, and diameters of testis and epididymis tubules in microns, of bearded seals of various ages. Twenty-five tubules from each specimen were measured to determine the mean. Not all tubules could be measured, due to distortions of preservation, but the spermatogenic stages in such tubules could be evaluated. An "X" indicates the presence of spermatids or spermia in the situation indicated.

Age	Testis length	Testis width	Diameter of testis tubules	Diameter of epididymis tubules	Spermatids in testis	Spermia in testis	Spermia in epididymis
years	mm.	mm.	$\mu$	$\mu$			
0.2	24	15	61	75			
1.3	25	15	67	87			
1.4	28	18	65	68			
2.2	35	24	...	...			
2.4	38	15	77	89			
4.9	32	18	88	187	X		
6.2	44	22	121	136	X		
7.3	43	28	149	213	X		
7.4	54	37	122	...	X		
7.4	46	33	...	...	...		
8.3	60	40	...	...	...		
10.1	64	38	193	322	X	X	X
Age 9+ to 16+ (av.)	56.4	34.8	142.9	184.8	X <sup>a</sup>	X <sup>b</sup>	X <sup>c</sup>
Specimens examined	19	19	14	10	14	14	12

<sup>a</sup>Spermatids present in all 14 specimens.

<sup>b</sup>Spermia present in 5 of 14 specimens.

<sup>c</sup>Spermia present in 3 of 12 specimens.

activity of testes of various ages, as this is reflected in stages of spermatogenesis, sizes of testes, and diameters of testis and epididymis tubules. It is apparent that there is a marked increase in activity in the early eighth year, and that the male probably breeds for the first time when seven years old.

The baculum, or penis bone, exhibits a spurt of growth in the sixth and seventh years (Fig. 2). This bone appears to attain almost its full length when the animal is seven years old, although the weight continues to increase in older seals.

Sexual maturity of the female is attained when the first ovulation occurs. Some development of follicles, both during and outside the breeding season, occurs in the years before maturity. The youngest female with any extensive follicular development was about five years old on July 3. Ovulation is succeeded by the development of the corpus luteum at the site of ovulation. This gland, or its regressed form, the corpus albicans, is thus an indication of maturity. Of four animals between six and eight years old, three were mature. The ovaries of the youngest, a seventh-year animal taken on August 8, showed an abnormal development of seven large follicles, which were from 7 mm. to 10 mm. in maximum

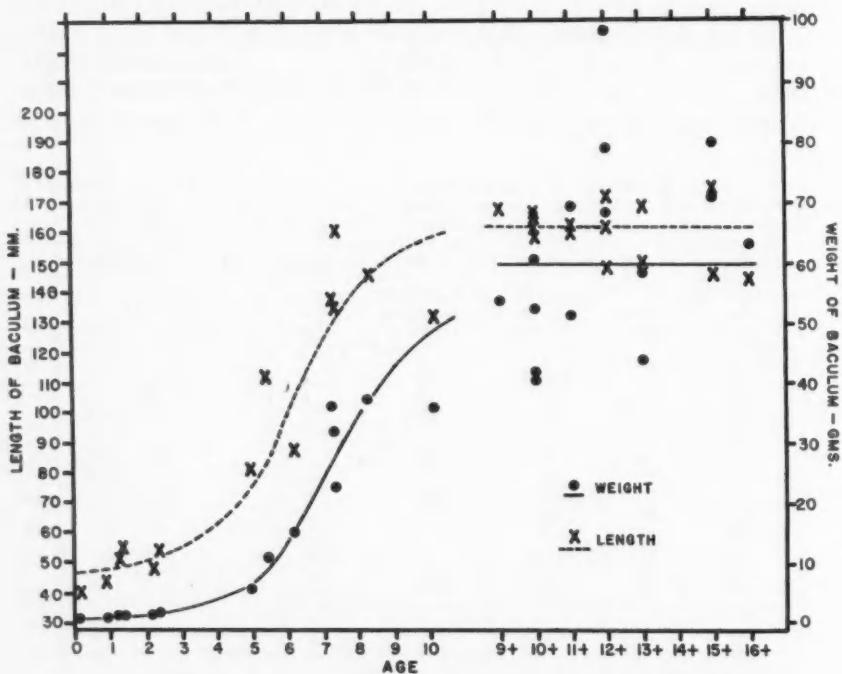


FIG. 2. Relation between size of baculum and age in years of the bearded seal. Animals with indicated ages from 9+ to 16+ years could not be fully aged, due to the loss through wearing of the first year's growth band on the claws.



diameter. Each of these presented the appearance of a small corpus luteum, with plications from the follicle wall and luteinization of the tissue. They were not true corpora lutea, since they had developed deep within the ovaries and could not have ruptured at the surface, nor did they resemble the luteinized follicles described by Laws (1956b) in the elephant seal, *Mirounga leonina*. Whatever their significance, they almost certainly reflect, if abnormally, the hormonal state of maturity. A seven-year-old female on April 29 showed several large follicles, up to 5 mm. in diameter, but no corpus luteum. The ovaries of another of the same age on May 9 were relatively inactive, but a corpus albicans of the previous year's ovulation, which had been unaccompanied by pregnancy, signified maturity. An animal killed in her eighth year on June 30 had been pregnant in her seventh year; one corpus albicans indicated that this pregnancy had probably resulted from her first ovulation.

Thus the limited evidence suggests that the male bearded seal is mature by age of seven and that the female may mature, on the average, when six years old. These are exactly comparable with the ages at maturity in the ringed seal (McLaren, in press). Further collections will undoubtedly establish a range of variation in these ages.

#### THE BREEDING SEASON AND THE SEXUAL CYCLE

The young bearded seal is, according to most accounts, born in April or May. Some variation in the timing of birth may be related to latitude. Thus Mohr (1952) considers that the birth season is earlier in northern European waters and off Newfoundland than in the higher arctic seas, and Sleptsov (1943) suggests that pupping occurs in March-April in the Okhotsk Sea, or even earlier in the southerly Tartar Straits. May 1 may be considered to be the average birth date in the eastern Canadian Arctic. The mating season according to some authors (Kumlien, 1879; Chapsky, 1938) occurs shortly after the period of birth. Sleptsov (1943), who amassed considerable material, believes that the bearded seal mates a full three months after the birth season, at the end of the moulting period.

The season of male rut is less subject to variation in timing than the season of ovulation, for the females of several species have been known to ovulate outside the breeding season (Hamilton, 1939; Rand, 1954; McLaren, in press). Five adult male bearded seals have been taken with spermia in the testes—on May 30, June 19 (2), July 2, and July 3. The epididymis of the May 30 specimen was unfortunately not collected, but scattered spermia in the *ductuli efferentes* suggest that the animal was potent. The epididymis tubules of one of the June 19 specimens were not fully packed with spermia, and the epididymis of the other was aspermous. Only scattered spermia were mixed with the spermatogenic cells and degenerate products in the July 3 specimen, while the epididymis of the July 2 male was devoid of spermia. No other testes taken between July 3 and October 8, including three taken in mid-July, were active. It is apparent that the series represents a decline in spermatogenic activity and that the peak of male potency occurs before June.

Measurements of testes and diameters of tubules demonstrate this same decline in activity in early summer. These measurements are displayed on Figure

3, and the freely drawn curve suggests the best estimate of the period of rut in May, shortly after the pupping season.

Chapsky (1938) and Sleptsov (1943) both suggest that the bearded seal produces one pup every second year. Neither speculates on the mechanism by which this two-year cycle, which is unique among the Phocidae, is established. The limited material of the present study suggests that the female may forego ovulation until after the breeding season of the male, when she has recently

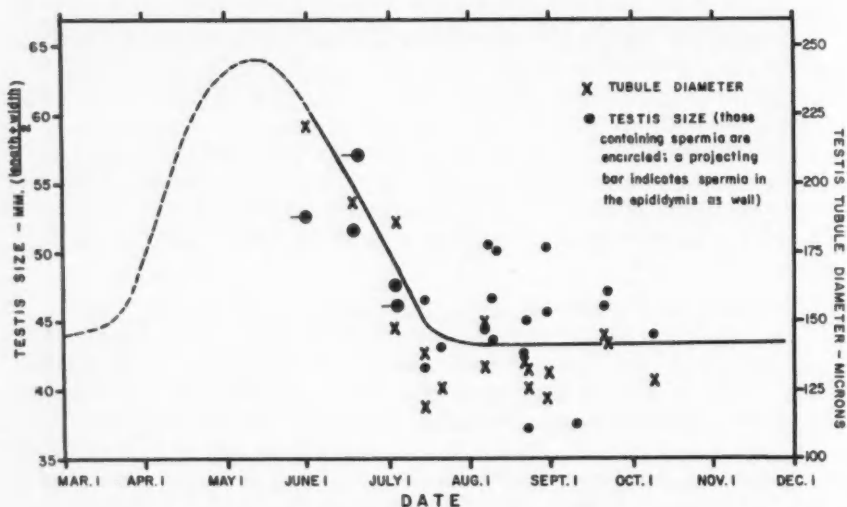


FIG. 3. The seasonal variation of testis size and testis tubule diameter in the bearded seal. The curve is drawn to indicate the presumed peak of sexual activity in May.

given birth to a pup. Thus, two specimens whose tracts showed placental scars of recent pregnancy were taken on May 30 and June 19. The ovaries opposite to those which controlled the previous pregnancies contained large follicles (the largest were 14 mm. and 11 mm. in the respective specimens) which had not yet erupted. Another recently pregnant female on July 6 had a very new corpus luteum; the granulosa cells of the follicle wall were streaming into the unfilled centre, and little luteinization of these cells had taken place. Other females in which no embryos were found were taken in July to September, with corpora lutea in various stages of development. Some were quite recent in appearance, while others were older and approached those of pregnant seals in degree of vascularization and connective tissue development. One specimen on July 29 was pregnant, with a very recently implanted embryo. Its corpus luteum was rather free of vascular tissue, suggesting that those females in which no embryos were found, and whose corpora lutea were of more advanced appearance, were pseudopregnant.

Embryos were removed from nine females in late July to late October, and these are listed in Table II. If we consider, from this small series of specimens, that the embryo implants around the beginning of August, a delay in implantation of about  $2\frac{1}{2}$  months is implied. Embryos of less than 1 mm. on July 29 and of 2-3 mm. on September 17 suggest that the period covering implantation is at least  $1\frac{1}{2}$  months. This probably reflects the length of the breeding season.

TABLE II. Size of embryos of the bearded seal in July to October. Embryos were measured in millimetres from tip of nose to tip of tail along curvatures and flexures.

Date	Geographical origin	Length
		mm.
July 29	Northern Foxe Basin	Newly implanted
August 22	Southwest Baffin Island	14.5
August 28	Northern Foxe Basin	120
August 29	Southampton Island	109
September 2	Ungava Bay	114
September 17	Northern Foxe Basin	2.5
September 20	Southampton Island	222
September 21	Northern Foxe Basin	86
October 29	Northern Foxe Basin	240

Sleptsov (1943) did not acknowledge delayed implantation of the embryo of this species, contrary to the findings of Chapsky (1938). Although Sleptsov dealt with a very large series of animals, he appears to have made some errors in his analysis of the material. He observed one case of apparent copulation on July 7, although active ovulation, as indicated by the presence of corpora lutea, had occurred in all specimens taken after the commencement of seal collecting in late May. He states that between June 1 and 31 the testes of all adult males were swollen, but emphasizes that only small quantities of spermia were observed in the ducts, while suggesting that this should not be taken as an indication that breeding has already occurred. To justify this view, he considers that there is probably never much ejaculate in the ducts of Phocidae in general, an assumption which is certainly not borne out by recent studies. It is quite apparent that Sleptsov's male specimens were passing out of rut, and that his female specimens had ovulated before the peak of supposed breeding activity in the second half of June to the second half of July. The large series of embryos which he removed in early stages of development indicates an average implantation time around the beginning of July, a full month before the suggested implantation time in the eastern Canadian Arctic. A delay in implantation of  $2\frac{1}{2}$  months would place the peak of the breeding season in the beginning of April; this coincides with his statements that the pup is produced in March or April in the Okhotsk Sea area.

Sleptsov reaffirmed his views on the timing of the breeding season of other Pinnipedia in a later paper (1948). In this study he examined female harp seals, for which there is very well documented evidence of ovulation shortly after the birth of the pup, and considered that this species, too, mated considerably later than had been supposed; obviously his views on reproduction of this species are also untenable.

## RELATIONSHIPS BETWEEN GROWTH AND SEXUALITY

At the time of Laws' (1956a) preliminary analysis of growth and sexuality in marine mammals, little information was available from published accounts of this species. Laws makes use of the findings of Chapsky (1938), whose seal ages were based on length-groupings, and subject to the inaccuracies of this technique.

Laws found that, on the average, 86% of the final length is attained at puberty in the females of the species which he studied. For the bearded seal, he gives figures of 79 inches (201 cm.) at puberty and 98 inches (249 cm.) at physical maturity; thus 81% of the final adult length is reached at the age of sexual maturity. It has been shown in the present study that the female ovulates for the first time when she is about six years old, when she would be (from Figure 1) about 210 cm. in length. It may be considered that females older than nine years have reached physical maturity; the average length of such females is about 230 cm. Thus, in the present material, the female at puberty appears to have reached fully 91% of the final adult length, a figure considerably in excess of that suggested by Laws.

Laws also relates the increase in length in the first year of life of the females of several species to their ages at sexual maturity. These are inversely proportional, the regression line plotted by Laws indicating that females maturing at the age of two years increase their length in the first year by about 80%, while females maturing at the age of six years have a length increment of about 20% in the first year. The female bearded seal, as suggested in Figure 1, increases from about 120 to 160 cm. in the first year, an increment of about 33%. This suggests an age of maturity at five years, whereas the actual age of sexual maturity observed in the small collections available is at six years.

## SUMMARY

1. The material on which this study is based was collected from 113 specimens of bearded seals in the eastern Canadian Arctic.
2. The method of aging from dentinal annuli in the canine teeth cannot be applied to the bearded seal, whose teeth are degenerate. Bands on the claws give a valid indication of age, up to 9 to 16 years, and 62 specimens were aged by this technique.
3. The bearded seal grows from about 120 cm. in nose-tail length at birth to a final adult length of about 235 cm., with little sexual difference.
4. The male matures at seven and the female at six years of age.
5. The pup is produced in April and May, averaging around May 1 in the eastern Canadian Arctic. The males are going out of rut in June and are probably most potent in mid-May. Females which have produced a pup probably forego ovulation until after the season of sexual activity of the males, thus establishing a two-year cycle of pup production.
6. The embryo implants during a period of at least 1½ months around the beginning of August, after a delay in development of about 2½ months.
7. The female at puberty has reached 91% of her final adult length, a somewhat greater development than the average of 86% which has been suggested for

other Pinnipedia. The females of other Pinnipedia have been used to establish a relationship between growth in the first year and age of sexual maturity. Females maturing at the age of six are expected to exhibit a length increment of about 20% in the first year; the bearded seal increases its length by 33%, and is thus somewhat at variance with the theory.

#### ACKNOWLEDGMENTS

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# Some Effects of Temporary Exposure to Low Dissolved Oxygen Levels on Pacific Salmon Eggs<sup>1</sup>

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## ABSTRACT

Eggs of the chum salmon (*Oncorhynchus keta*) were exposed to various constant levels of dissolved oxygen for a period of seven days. The procedure was repeated with fresh egg samples at various developmental stages. Temperatures were constant at 10°C. from fertilization to hatching. Estimates of oxygen consumption uninhibited by low dissolved oxygen levels were obtained at various stages of egg development for whole eggs and also on the basis of the weight of larvae, excluding the yolk. Eggs were most sensitive to hypoxia between 100–200 Centigrade degree-days and compensated for reduced oxygen availability by reducing the oxygen demand and rate of development. Very low oxygen levels at early incubation stages resulted in the production of monstrosities. At about the time the circulatory system becomes functional the compensatory reduction in rate of growth under hypoxial conditions is reduced, but eggs no longer survive extreme hypoxial conditions. Eggs subjected to low dissolved oxygen levels just prior to hatching hatch prematurely at a rate dependent on the degree of hypoxia. The maximum premature hatching rate corresponded approximately with the median lethal oxygen level. Estimated median lethal levels rose slowly from fertilization to hatching. Oxygen consumption per egg rose from fertilization to hatching while the consumption per gram of larval tissue declined from a high to a low level at about the time of blastopore closure. Subsequently, a slight rise in the rate occurred up to a level which was more or less constant to hatching. "Critical" dissolved oxygen levels were calculated and they appear to define the oxygen level above which respiratory rate is unmodified by oxygen availability. Critical levels ranged from about 1 p.p.m. in early stages to over 7 p.p.m. shortly before hatching.

## INTRODUCTION

LABORATORY EXPERIMENTS have been conducted on eggs of the chum salmon (*Oncorhynchus keta*) in order to investigate effects of a low dissolved oxygen

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environment on their development and survival. During recent years a program of field studies at the Fisheries Research Board of Canada's Nanaimo Station has investigated factors which influence the success of incubation and emergence of free-swimming pink (*O. gorbuscha*) and chum fry (Neave, 1947; Wickett, 1954). Wickett further attempted to define the reasons for high pre-eyed egg loss observed in nature on the basis of the relations between the velocity and oxygen content of sub-surface water in the gravel. Following and in conjunction with the latter, this investigation was begun in order to determine the responses of the eggs themselves to variations in oxygen availability and to assess the manner in which such variations might produce mortality.

The availability of oxygen to salmon eggs may be considered to be dependent primarily on the oxygen pressure in the microenvironment surrounding each egg. Whereas temperature may effect the oxygen pressure in the microenvironment, it will also influence the physiological state of the egg and its potential rate of oxygen utilization. Thus, Lindroth (1942) demonstrated that for Atlantic salmon (*Salmo salar*) eggs just prior to hatching, a temperature of 17°C. resulted in oxygen consumption at the rate of about 29 cc./kg./hr. (sustainable by a dissolved oxygen content of not less than about 8.7 p.p.m. or 89% of saturation or greater). By comparison, at 5°C. the rate of consumption was about 16 cc./kg./hr. (sustainable by a dissolved oxygen content of not less than about 5.7 p.p.m., or 45% of saturation or greater). The utilization rate itself may influence the oxygen content of the water if the rate of replacement of the microenvironment is insufficient to provide for the full utilization potential. Investigations by Wickett (loc. cit.), for example, indicated that to satisfy the potential oxygen demand of pre-eyed chum salmon eggs at 8°C., the oxygen content may vary between the equivalent of air saturation and 1.67 p.p.m., depending on the velocity of the perfusing water. Again, under the same conditions not even air-saturated water will sustain the egg if the apparent<sup>2</sup> velocity of the water drops below approximately 5 mm./hr.

Comprehensive reviews concerning the metabolism and development of, and the influence of the environment on teleost eggs have been published by Hayes (1949) for salmonids and by Smith (1957).

In studying the response<sup>1</sup> of salmon eggs to variations in their environment, it is important to recognize that one is dealing with an organism which is changing day by day. Not only are growth and differentiation progressive, but the rates governing these attributes also may be modified by the environment. As anatomical differentiation proceeds, the response of the animal to its environment may vary not only progressively but also by periods of susceptibility associated with variable sensitivity. In order to evaluate the effects of a low dissolved oxygen environment, a proper procedure was considered to be that of exposing eggs to various temporary low dissolved oxygen levels to determine the sensitivity of the egg, in terms of susceptibility, at various stages of development between fertilization and hatching.

<sup>2</sup>See Wickett (1954). The true velocity of a fluid flowing through granular material is impossible to determine, and an estimate of the true value is equal to volume discharge per unit time divided by the cross-sectional area of the gravel bed.



## MATERIALS AND METHODS

The apparatus consisted of a device for providing continuous supplies of air-saturated and deoxygenated water. The two supplies were combined in fixed proportions to provide a series of six constant levels of dissolved oxygen at constant temperature.

Deoxygenated water was provided by a "stripping column", a modification of apparatus described by Fry (1951). Water was allowed to fall through a column of glass chips providing high water-gas surface interfaces. An atmosphere of nitrogen passing up the column permitted the water to equilibrate at the interfaces with the high nitrogen gas content, removing the oxygen. Air-saturated water was provided in the same manner by leading compressed air through a similar column (Fig. 1).

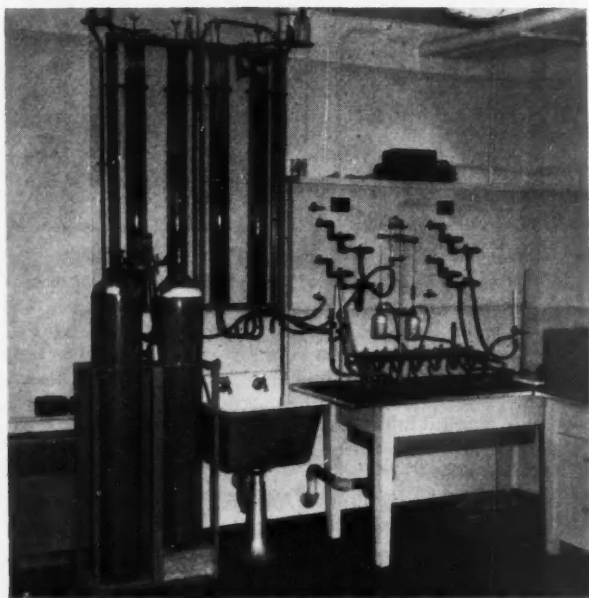


FIG. 1. Equilibration columns used for supplying deoxygenated and air-saturated water. Water is piped to the tops of the columns, falls through the glass chips and is collected at the bottom. Nitrogen gas is passed up through the two left-hand columns, and compressed air through the right-hand pair.

The two water supplies were then led into a constant temperature bath where temperature equilibration was effected in plastic-lined aluminum tubing. From this point the two water supplies were led to mixing valves adjusted to provide prescribed oxygen levels, thence back to the egg chambers housed in the same constant temperature bath (Fig. 2).

Eggs were fertilized and cultured at the Nanaimo Station (Series B-E, Table II), and at Nile Creek Field Station (Series A), for later transfer. The

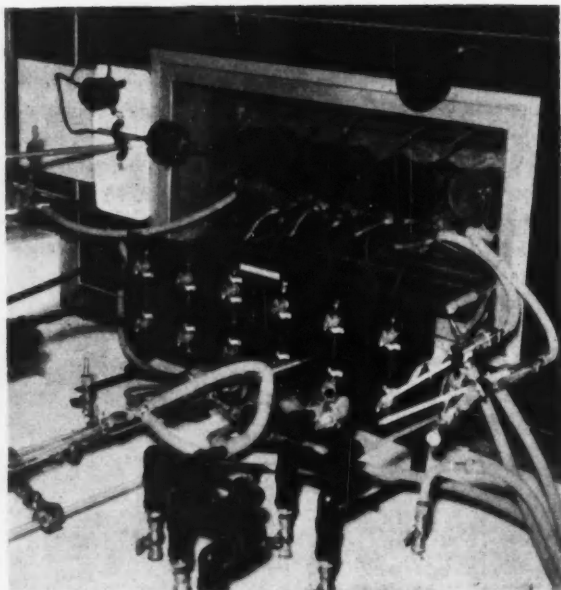


FIG. 2. The two water supplies from the columns are led through bubble traps and into temperature equilibration coils in the constant temperature bath. From there they are led into two manifolds under the bank of mixing valves, through the mixing valves where they are re-combined in prerequisite proportions and delivered to the bottom of the egg chambers where the water passes up through a single layer of eggs to the overflow. The head bottles are attached to the manifolds and provide a constant head at the egg chambers.

first series was conducted in the winter of 1953-54; the remaining four series were completed in the winter of 1954-55.

At the start of an experiment, samples of eggs of known developmental age were removed from incubation trays and carefully inserted into the six experimental chambers, each chamber being maintained at a fixed oxygen level for a period of seven days. The water passing through the single layer of eggs had an apparent velocity of about 850 mm./hr. Egg samples were then returned to individual incubation baskets and held in one hatchery trough until hatching was complete. The temperature to which the eggs were exposed was held constant throughout the total incubation period including the interval of exposure to the low dissolved oxygen conditions.

Dissolved oxygen determinations were carried out in the usual manner, employing the unmodified Winkler titration method. Determinations were made on a 50-ml. aliquot, titrating with 0.01N thiosulphate at those levels of 5 p.p.m. dissolved oxygen or greater. Below 5 p.p.m. dissolved oxygen, titrations were conducted with 0.005N thiosulphate from a 5-ml. microburette.

In each of four tests on oxygen consumption, 50 eggs were set out on a nylon net platform expanded within an aspirator bottle of about 600 ml. capacity. Water of known oxygen content was allowed to overflow through the bottle until at least two volumes had been exchanged. The lower orifice was closed off and a mineral oil seal of approximately 2 cm. depth was poured into the neck of the bottle. The bottle was then immersed in a constant temperature bath and the contents were slowly circulated using a rheostat-controlled electric stirrer with a length of straight glass rod projecting through the oil seal. Eggs treated in this fashion were allowed to respire until an estimated 2 p.p.m. dissolved oxygen had been removed from the closed bottle. The contents were sampled for dissolved oxygen and the volume of water used in the closed bottle was measured.

For convenience, several terms have been used to describe the young fish throughout development which require explanation. Whereas "embryo" is used to denote the unhatched fish, "larva" is used to denote the young fish separated from its yolk. "Pre-hatching stage" refers to the period of ten days prior to the mean hatching date of a sample of eggs.

Embryo weights were obtained by slitting the egg capsule and dissecting each larva away from the yolk. The larvae were hardened in 10% formalin, dried of external moisture on filter paper, and weighed on an analytical balance. A comparison of fresh and preserved larvae was made on pre-hatching stage embryos and the percent loss in weight through dehydration was applied to the earlier stages as a correction factor. Average larval weights were calculated on the basis of the weights of samples of 7 to 10 larvae.

## RESULTS

Exposure of eggs at various developmental stages to low oxygen produced three gross responses: production of monstrosities, delay in the rate of development, and mortality. The distribution of hatching times in each sub-sample of eggs was found to be skewed. The best measure of central tendency was that provided by the median hatching time. Where approximately 50% or more of a sample of treated eggs survived to hatch, the net delay in days to the median hatching date has been calculated using the control groups as a standard. In the remaining cases complete or nearly complete mortality prohibited such estimates. Temperatures associated with the experiments and the incubation periods for control samples are listed in Table I.

"Degree-days" have been employed to express the relationship of temperature and incubation time where one degree-day is equivalent to exposure to a

TABLE I. Temperatures and incubation periods for the experimental controls.

Series	A	B	C	D	E
Av. rearing temperature, fertilization to hatching, °C.	5	9.8	9.9	9.7	9.7
Av. experimental temperature, °C.	4.8	10.7	10.4	10.2	10.1
Interval from fertilization to hatching, degree-days	...	510.5	512.7	563.3	588.9
Time to median hatching date, days	...	52.1	52.0	57.5	60.8

temperature of one Centigrade degree (above 0°C.) for one day (see Hayes, 1949; Seymour, 1956). Measures of the response of eggs to the various levels of dissolved oxygen imposed at several stages of development are listed in Table II.

It may be seen from examination of Table II that developing eggs are not

TABLE II. Results of exposure of samples of chum salmon eggs to various levels of oxygen saturation. Series A was carried out at 5°C. on sub-samples of 10 eggs, the remaining series were conducted at 10°C. on sub-samples of 20 eggs. In each series sub-sample 6 is a control at oxygen levels approximating air-saturation at the temperatures involved. The alevins marked with an asterisk (\*) showed abnormal development.

SERIES A. Development stage—just prior to and during hatching.						
Sub-sample	1	2	3	4	5	6
Av. experimental O <sub>2</sub> level, <i>p.p.m.</i>	0.26	0.29	1.41	1.97	4.20	12.47
No. of dead eggs at end of experiment	7	8	1	0	0	0
No. prematurely or unsuccessfully hatched	3	1	0	0	0	0
No. hatched in test period	3	2	7	6	4	3
No. of dead alevins at end of the hatch	3	1	1	0	0	0
Total live alevins hatched	0	1	7	10	10	10
SERIES B. Developmental stage—121.2 degree-days (24% of control incubation period).						
Sub-sample	1	2	3	4	5	6
Av. experimental O <sub>2</sub> level, <i>p.p.m.</i>	0.25	0.29	0.72	0.92	2.15	10.17
No. of dead eggs at end of experiment	0	0	1	2	0	0
No. prematurely or unsuccessfully hatched	2	0	0	2	0	0
No. of dead alevins at end of hatch	2*	0	0	3	0	0
Live alevins hatched	17*	20*	17	14	20	20
Median hatching date, January	12.5	12.0	12.9	9.8	7.4	2.1
Delay in hatching, days	10.4	9.9	10.8	7.7	5.3	0
Time from fertilization to median hatching date, days	62.5	62.0	62.9	59.8	57.4	52.1
SERIES C. Developmental stage—205.8 degree-days (40% of control incubation period).						
Sub-sample	1	2	3	4	5	6
Av. experimental O <sub>2</sub> level, <i>p.p.m.</i>	0.20	0.32	0.61	0.87	1.67	10.20
No. of dead eggs at end of experiment	20	20	10	0	0	0
No. prematurely or unsuccessfully hatched	0	0	0	0	0	0
No. of dead alevins at end of hatch	0	0	0	0	0	0
Total live alevins hatched	0	0	8	20	20	20
Median hatching date, January	...	...	12.3	11.1	8.5	2.0
Delay in hatching, days	...	...	10.3	9.1	6.5	0
Time from fertilization to median hatching date, days	...	...	62.3	61.1	57.5	52.0
SERIES D. Developmental stage—296.1 degree-days (53% of control incubation period).						
Sub-sample	1	2	3	4	5	6
Av. experimental O <sub>2</sub> level, <i>p.p.m.</i>	0.37	0.52	0.81	1.94	3.04	10.28
No. of dead eggs, end of experiment	18	11	1	0	0	0
No. prematurely or unsuccessfully hatched	0	0	0	0	0	0
No. of dead alevins at end of hatch	0	0	0	0	0	0
Total live alevins hatched	2	8	19	20	20	20
Median hatching date, January	...	13.3	12.3	9.8	8.6	7.5
Delay in hatching, days	...	5.8	4.8	2.3	1.1	0
Time from fertilization to median hatching date, days	...	63.3	62.3	59.3	58.6	57.6
SERIES E. Developmental stage—452.4 degree-days (77% of control incubation period).						
Sub-sample	1	2	3	4	5	6
Av. experimental O <sub>2</sub> level, <i>p.p.m.</i>	0.36	0.52	0.81	1.81	4.05	10.14
No. of dead eggs at end of experiment	19	16	10	0	0	0
No. prematurely or unsuccessfully hatched	1	1	6	2	1	0
No. hatched during the test period	1	1	5	2	1	0
No. of dead alevins at end of hatch	1	2	6	0	0	0
Total live alevins hatched	0	1	0	20	20	20
Median hatching date, January	...	...	5.0	12.3	11.6	10.8
Delay in hatching, days	...	...	*	1.5	0.8	0
Time from fertilization to median hatching date, days	...	...	55.0	62.3	61.6	60.8

\*These eggs hatched prematurely, 5.8 days earlier than the controls.

equally affected at different stages by similar hypoxial environments. The three major indications of stress, production of monstrosities, variation in hatching rate, and mortality are treated separately in the following sections.

#### PRODUCTION OF MONSTROSITIES

In Series B, undertaken 12 days following fertilization, moderate to low mortality occurred in the sub-samples from 0.25 to 0.92 p.p.m. dissolved oxygen. Examination of the eggs in this series was carried out on the 27th day after fertilization, following the period of low-oxygen exposure between the 12th and 19th days. Eggs from the control (sub-sample 6) corresponded in development with those in the balance of the egg stock, characterized by the heart formed and beating, the eyes pigmented, and the vitelline vessels well established. Development in sub-sample 5 was only slightly less than that in the control. However, in the remaining sub-samples, the vitelline circulation indicated considerable retardation in development with the vitelline vein in sub-sample 4 enclosing an area devoid of vascularization equivalent to a solid angle of about  $45^\circ$ . A progression in retardation was evident right through to sub-sample 1 in which the position of the vitelline vein was slightly above the equator of the yolk and the enclosed area free of vascularization. A progression in degree of eye pigmentation was also evident in sub-samples 4 to 1, no pigmentation being discernible in the latter.

It has been well substantiated that the period of development during which the blastoderm is overgrowing the yolk is associated with marked fragility of the egg (Hayes, 1949). It is quite possible that the mortality which occurred in Series B, sub-samples 1 to 4, could be ascribed in part or entirely to such fragility.

However, in the two sub-samples in Series B subjected to less than 0.3 p.p.m. dissolved oxygen, of 40 eggs involved, 39 of the alevins which hatched were abnormal in form. From gross observation these were characterized by a shortening of the vertebral column posteriorly (Fig. 3). The final form suggests that the low-oxygen environment was imposed upon the embryo at a time when somite formation had proceeded posteriorly to the region of the insertion of the dorsal fin and interruption of somite formation left the embryo blocked at that stage of segmentation, with subsequent appendages being laid down on the incomplete vertebral structure (for an extensive treatment of the experimental production of deformities see Stockard, 1921).

The plasticity and survival apparent in the egg samples at this early stage of development were not maintained in the next experimental stage. Oxygen levels slightly higher than 0.3 p.p.m. (0.32 p.p.m., sub-sample 2, Series C), 22 days after fertilization, produced complete mortality in contrast to successful but abnormal development in Series B.

#### VARIATION IN HATCHING RATE

In Series B to E, variations in the rate of hatching have been calculated as the difference in days between the median hatching date of the controls and that of the other sub-samples. If air-saturation in the controls may be regarded as the condition affording best opportunity for development and survival, then

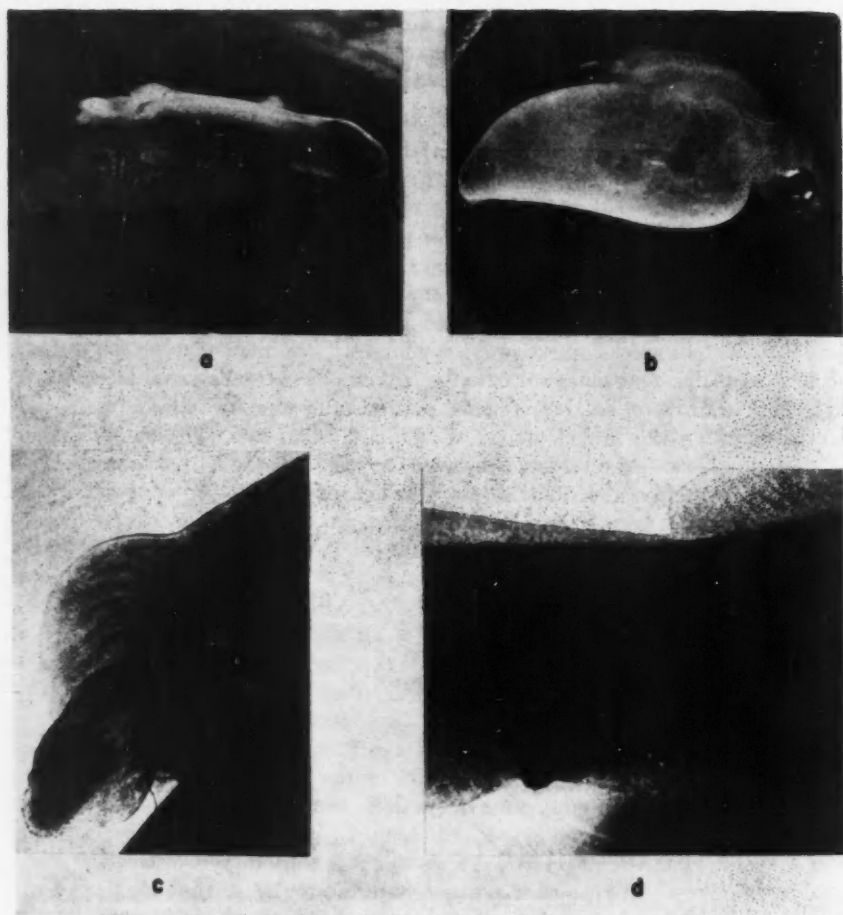


FIG. 3. Deformity resulting from exposure of chum salmon eggs to hypoxia at an early incubation stage: (a) and (b) hatched alevins showing posterior truncation; (c) alevin showing the location of the caudal and pelvic fins immediately beneath the dorsal fin—there is also an oblique displacement of the caudal fin from the dorso-ventral axis; (d) a normal alevin photographed in the same area as (c) illustrating the extreme truncation of the posterior portion of (c).

variations in hatching rate may be regarded as a measure of sub-lethal stress on the developing embryo. The diverse and complex nature of the relationship between oxygen level and developmental stress is illustrated in Figure 4. At the first experimental stage (12 days or 121.2 degree-days), sub-lethal stress reaches a maximum at about 0.3 p.p.m. dissolved oxygen, resulting in a delay in hatching of about 10 to 11 days after an exposure of one week to the hypoxial conditions.

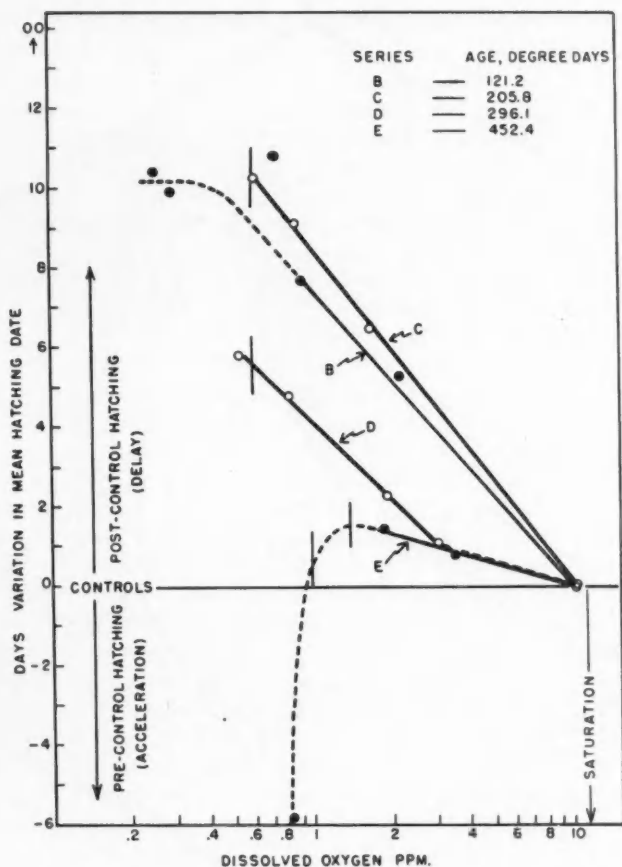


FIG. 4. The relationship between dissolved oxygen level to which developing chum salmon eggs were exposed for a period of 7 days and the variation from the normal or control incubation period at 10°C. The differences in hatching rate are regarded as a measure of the stress applied to the eggs by low-oxygen conditions at the four developmental stages examined. Not all eggs hatched at every point; the approximate position of the median lethal low oxygen level is indicated on each line by a vertical bar. Although almost all eggs hatched at the two lowest oxygen levels in Series B, the resulting alevins were deformed and considered inviable.

It is within this range that abnormal development occurred. In the next series (22 days or 205.8 degree-days) the slope of the line is increased, a unit decrease in oxygen level placing a greater stress on the embryo than at an earlier developmental stage. In Series D (32 days or 296.1 degree-days) the relationship de-



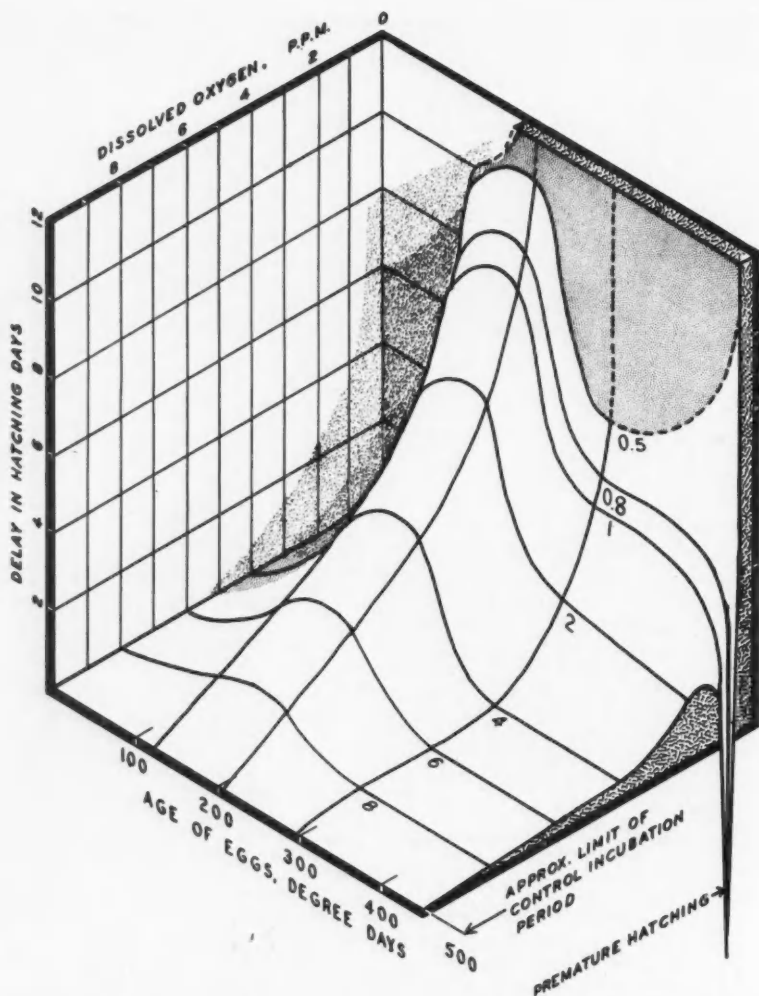


FIG. 5. Variation in hatching rate of samples of chum salmon eggs reared at 10°C. resulting from a 7-day exposure to prescribed oxygen levels at intervals throughout the incubation period. Variation from the control hatching rate, represented by the extent of the "hump", is regarded as a measure of stress (see text). (Drawn by D. Denigh.)

scribes a break in linearity at about 3 p.p.m. dissolved oxygen, with the stress at all levels considerably reduced from that of the two earlier series. In the final series (48 days or 452.4 degree-days), the change in slope is complete with the stress tending toward a minimum. However, the degree of hypoxia which the



developing embryo may tolerate is considerably reduced and a new condition is produced in which there is a tendency for eggs to hatch prematurely when subjected to low oxygen levels.

To provide a visual indication of the complex variations in response to low oxygen as measured by delayed hatching rate, a three-dimensional diagram has been constructed in Figure 5 by isometric projection of surfaces from Figure 4. The diagram may be interpreted as follows: comparing the hatching rates of control egg samples subjected to oxygen levels approximating air-saturation (10 p.p.m.) with hatching rates at lower oxygen levels (Series B-E, Table II), surfaces have been constructed by scaling off the variations in hatching rate (mostly delay) from Figure 4 at the oxygen levels listed in that figure and at the four incubation stages examined (Series B-E). Dashed lines infer that stress is becoming infinite, in other words, mortality is complete or nearly complete. Increases in the vertical dimension of the solid correspond to increases in the stress resulting from exposure to hypoxial conditions. A period of maximum stress occurs between 100 and 200 degree-days of development. Stress also increases at all levels below air-saturation. Acceleration of hatching results in premature hatches when pre-hatching stage eggs are exposed to oxygen levels below air-saturation. This effect is maximized at about 1 p.p.m. dissolved oxygen at 10°C. The incubation period of the controls is equivalent to about 500 degree-days.

Other work with salmonid eggs reared at various levels of dissolved oxygen has demonstrated no significant variation in hatching rates (E. T. Garside, personal communication). It is possible that eggs developing at oxygen levels below air-saturation may acclimate to a range of those levels by proliferation of accessory respiratory surfaces in the manner described by Smirnov (1953). It is suggested that eggs acclimated to low oxygen conditions would not respond to hypoxial conditions in the same manner as eggs reared at oxygen levels approximating air-saturation by virtue of the ability of the former eggs to extract oxygen with greater efficiency at lower environmental oxygen levels.

If pre-hatching stage eggs are exposed to low-oxygen conditions, premature hatching occurs, illustrated by examination of Series A and E. Figure 6 illustrates that this rate of hatching is greatest at dissolved oxygen levels of about 1 p.p.m. In both series premature hatching is accompanied by mortality. The incidence of mortality at the lowest dissolved oxygen levels diminishes to zero between 1-2 p.p.m. dissolved oxygen.

#### MORTALITY

Since a limited number of experimental oxygen levels were set up to examine the effects of a large range of hypoxial conditions from very low levels to air-saturation, the data do not lend themselves to calculation of values describing median lethal effects. However, several general observations may be made by examination of Table II.

Series B, the earliest developmental stage examined, did not sustain 50% mortality in any of the sub-samples. However, as all alevins hatching successfully after exposure to the two lowest dissolved oxygen levels (0.25, 0.29 p.p.m.) were

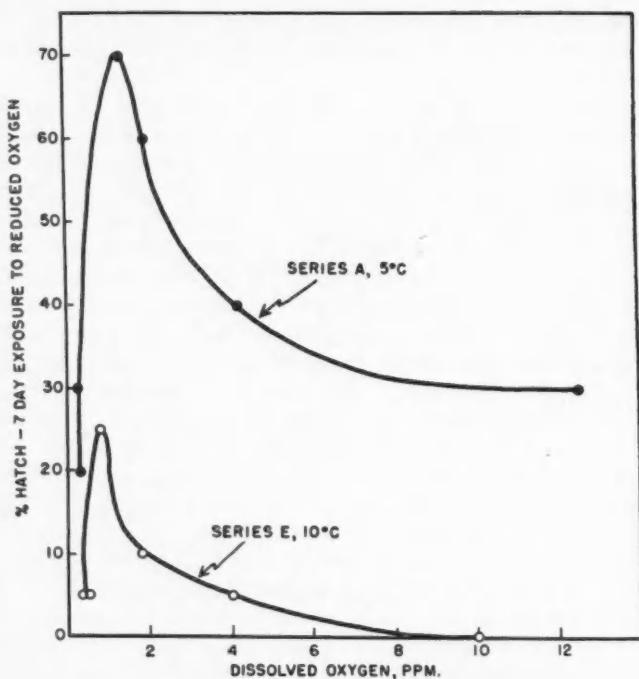


FIG. 6. A comparison of the rates of hatching of eggs subjected to dissolved oxygen levels below saturation. The right-hand points on each curve correspond to the controls. Premature hatching is maximized in both series at about 1 p.p.m. dissolved oxygen. The difference in the magnitude of the hatches between the two series may be concerned with temperature differences but is more probably a result of the eggs in Series A being of a more advanced stage when the experiment started.

deformed and unable to move, even 53 days after their median hatching date, they may be considered to have been inviable. A median lethal dissolved oxygen level could be assumed to be at a level greater than 0.29 p.p.m. dissolved oxygen. Estimates of median lethal levels by inspection are presented in Table III for the Series B to E. (See Fig. 8.)

TABLE III. Median lethal dissolved oxygen levels for chum salmon eggs exposed to hypoxial conditions for a period of 7 days. The values are estimated by inspection from Table II.

Series	Age of eggs after fertilization	Age of eggs	Approx. range of oxygen levels	Estimated median lethal oxygen level
	<i>days</i>	<i>degree-days</i>	<i>p.p.m.</i>	<i>p.p.m.</i>
B	12	121.2	0.3-0.7	0.4
C	22	205.8	0.5-0.9	0.6
D	32	296.1	0.5-0.8	0.6
E	48	452.4	0.8-1.8	1.0-1.4

## CHANGES IN OXYGEN CONSUMPTION THROUGHOUT DEVELOPMENT

For Series B to E, estimates of oxygen consumption were obtained by allowing samples of 50 eggs to respire in a closed volume of water. The change in oxygen content was used to calculate rates of oxygen uptake listed in Table IV.

Rates of consumption are illustrated in Figure 7.

TABLE IV. Rate of oxygen uptake of chum salmon eggs (av. radius 0.37 cm.) at four developmental stages at 10°C. The oxygen consumption values in  $\text{mm}^3/\text{egg}/\text{hr.}$  are for comparison with other literature; values in  $\text{mm}^3/\text{g.}/\text{hr.}$  are based on the weight of living material, not including the yolk.

Age of eggs	Oxygen in closed system at times:		Mean larval weight	Oxygen consumption per hour		
	$t_0$	$t_1$				
<i>degree-days</i>	<i>p.p.m.</i>	<i>p.p.m.</i>	<i>g.</i>	<i>mg./egg</i>	<i>mm.<sup>3</sup>/egg</i>	<i>mm.<sup>3</sup>/g.</i>
121.2	10.12	8.70	0.0023	0.00093	0.68	295.1
268.2	9.91	5.84	0.0155	0.00219	1.60	103.1
353.0	10.41	8.11	0.0231	0.00381	2.78	120.4
452.4	10.25	8.23	0.0290	0.00521	3.80	131.2

## DISCUSSION

Hayes, Wilmot and Livingstone (1951) present evidence illustrating that oxygen consumption of incubating eggs of *S. salar* at 10°C. may be fitted to the equation

$$\log y = k_0 + k_1 \log (x - 9)$$

where  $y$  = oxygen consumption

$x$  = number of days after fertilization.

The constant, 9 days, is equivalent to the time of establishment of the embryonic axis. From inspection, the present consumption values follow the same type of relationship as those of Hayes *et al.*; however, the  $k_0$  value of the present series appears to be greater and the last determination tends to inflect. To effect a comparison, a correction may be made to bring egg weights into agreement. Eggs in the present series averaged 7.4 mm. in diameter as compared to a probable value of 6.0 mm. for those of Hayes and his co-workers. Relating the rate of metabolism at comparable ages to the surface areas (Krogh, 1941), consumption rates are between two to three times those of Hayes in the early stages, and are consistently higher throughout development. By comparison with data of Privolnev (see Hayes *et al.*, 1951) Hayes concludes that the oxygen consumption per gram of living tissue in early stages is not constant but declines with development. This conclusion is borne out by the present results (see Fig. 7) where consumption per gram of larval tissue declines from 295 to 103  $\text{mm}^3/\text{g.}/\text{hr.}$  between 121 and 268 degree-days development. Data of Hayes *et al.* are presented in Figure 7 for comparison. Whereas Hayes suggests that their data are apparently linear and constant (from 19 days until hatching, at 10°C.), in view of the evidence for curvilinearity and the decline in oxygen consumption from early stages among chum salmon eggs, a liberal re-interpretation of their results (Fig. 7) would suggest a trend similar to our own findings. It must be acknowledged, however, that a smaller number of observations are represented over the same range of ages in our own data. In arriving at

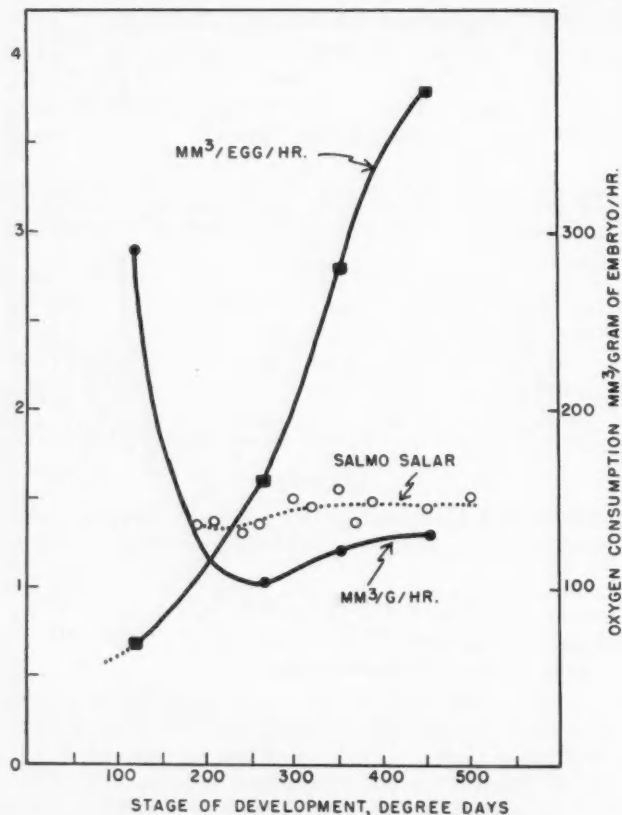


FIG. 7. Oxygen uptake of chum salmon eggs based on total egg weight and embryo weight less yolk. Compared with the latter are data for *Salmo salar* from Hayes, Wilmot and Livingstone (1951), and the interpretation of the trend in these data is our own.

estimates of the oxygen consumption per gram of larval tissue, the greatest potential source of error is found in weighing the embryos. If the high consumption value found for embryos at 121.2 degree-days development were attributed to error in this regard, it would be necessary to assume that the actual larval weight would be approximately 2.3 times greater than the measured weight to reduce the consumption value calculated for this stage to the approximate level of the remaining stages. Such a high weighing error is not considered plausible and the high consumption value for the early embryo is therefore not considered to be spurious. Oxygen consumption per egg for the chum salmon eggs is higher at all ages than comparable ages of Atlantic salmon, whereas the consumption per gram of larval tissue is lower than that of Atlantic salmon (from about 200 degree-days onward). The apparent contradiction suggests that the

metabolism and growth of the former in earlier stages is greater than in Atlantic salmon. Support for this assumption is suggested by the differences in consumption per gram of larval tissue which may reflect greater embryo weights at comparable ages in the chum salmon.

#### VARIATION IN HATCHING RATE

Within the range of temperatures employed in Series B to E, it may be assumed that the development rate as measured by *temperature times time* in days is a constant. However, the incubation periods of the controls in Series B to E exhibit increasing values which are disproportionate to the effects which would be expected from such slight average temperature differences throughout incubation. An uncontrolled variable associated with the development of the eggs was the length of time in which the egg stock was confined to the hatchery tray prior to the withdrawal of samples of eggs for each of the experimental series from B to E. Thus, Series B to E were incubated for 12, 22, 32 and 48 days in the hatchery tray prior to experimentation. Since essentially there is no difference between the mean hatching dates of the controls in Series B and C, the delay in hatching rate in the egg stock is assumed to have manifested itself between the 22nd and 32nd day of development, the latter being the age of Series C at which departure is first evident. In view of the fact that delay in hatching may be caused by exposure to low-oxygen conditions probably at any level below air-saturation at 10°C. (see Fig. 4), it appears reasonable to imply that the variations in rate of development might be explained by a progressively increasing competition for oxygen in the incubating egg stock. Evidence toward this conclusion could be based on a comparison of the period to 50% hatch in Series E with that of the stock which it should approximate. Although an exact record of the latter was not obtained, there is sufficient evidence to indicate that it was within one day of the period for the Series E control.

A variable sensitivity to external stimuli in developing salmon eggs has been noted by numerous investigators (Stockard, 1921; Devillers and Rosenberg, 1953). Battle (1944a) summarizes some of these responses including those from light, pressure, heat, cold, mechanical and electric shock and chemical action. Responses of eggs to such stimuli vary according to developmental stage. In general, it appears that susceptibility rises after fertilization, reaches a peak and begins to decline at a stage coincident with the closure of the blastopore. A second period of increased susceptibility has been found by others to be initiated in the latter part of the incubation period, reaching a peak at about the time of hatching.

In the present study, the effects of temporary low oxygen environments imposed for a period approximating  $\frac{1}{4}$  of the incubation period were also indicative of a variable response to an external stress, dependent for its magnitude on the age of development. It is probable that the early period of maximum susceptibility is coincident with the growth of blastoderm over the yolk and closure of the blastopore. No increase in susceptibility of pre-hatching stage eggs, as measured by delay in hatching rate, is indicated in the present tests. However, it is conceivable that the higher oxygen requirements per egg at

pre-hatching stages could easily create a local hypoxial environment providing conditions which would have been quite innocuous at earlier stages.

Hayes *et al.* (1951) considered the possibility that eggs exposed to lowered oxygen levels may incur an oxygen debt. Their evidence indicates that no debt was repaid after exposure of eggs to hypoxial conditions and led them to suggest that lowered oxygen supply may retard the rate of metabolism, or that an anaerobic mechanism may function under such conditions. The present evidence supports the former consideration. Furthermore, the reduction in metabolic rate which must be coincident with the observed deceleration in growth is greatest not only at the lower oxygen levels but also at the period of maximum egg fragility corresponding approximately with the period of blastoderm overgrowth and closure of the blastopore. Smith (1957) cites evidence that the glycolytic system, tricarboxylic acid cycle and cytochrome system are functional in intermediary metabolism of developing *Oryzias* eggs. Other evidence is presented indicating that carbohydrate is utilized during short periods immediately following gastrulation and during the hatching period for eggs of *Salmo irideus*. The capacity for anaerobic glycolysis is also stated to rise steadily throughout development. In view of this evidence the possibility that eggs subjected to low oxygen conditions may develop an oxygen debt can not be denied.

#### MORTALITY

In general, the results tend to indicate a slow but steady increase in the incipient low oxygen lethal level throughout development. Early stages exhibit a plasticity in which development may decelerate virtually to zero under extreme hypoxial conditions. In later stages this plasticity is lost and oxygen levels which would produce no more than a cessation of development at earlier stages become rapidly lethal.

Field sampling of eggs in natural redds by Wickett (1954) has indicated that high losses may be experienced in the pre-eyed stage. Wickett has developed methods of sampling for dissolved oxygen in sub-surface gravel and his work provides evidence that conditions recorded for the water flowing over spawning gravel may have no bearing whatsoever on conditions influencing eggs within the gravel. From consideration of the several variables influencing oxygen uptake in the gravel, Wickett arrived at a relationship providing a measure of sufficiency of oxygen supply. When the number of eggs normal to the direction of flow is considered, the following equation may be applied:

$$v (DO - C) = K$$

where  $v$  = apparent velocity of the perfusing water

DO = dissolved oxygen present

C = critical dissolved oxygen level

For a single chum egg at 8°C. with an uptake of 0.0003 mg./egg/hr., one of the asymptotes of the relationship is 1.67 p.p.m. dissolved oxygen, equal to the critical dissolved oxygen level calculated after Krogh (1941). Wickett's eggs were at a stage of development equivalent to 48 degree-days. The value presented, 1.67 p.p.m., represents the amount of dissolved oxygen present in the perfusing

water which is just sufficient to provide one egg, normal to the direction of flow, with sufficient oxygen at excess water velocity so that it may respire at an unmodified rate.

With Wickett's evidence, the following assumption is made. Early developmental (pre-eyed) mortality is undoubtedly associated with hypoxial conditions in the gravel, in the majority of cases brought about through a low apparent velocity or low dissolved oxygen content of water percolating through the gravel. Early developmental stages have a plasticity which compensates for hypoxial conditions by a marked reduction in rate of development. Such hypoxial conditions might continue for an extended period at low temperatures in nature (e.g. two months at 0-5°C.). This compensatory cessation in development could ultimately be lethal, and eggs which may have lived for a period longer than that suggested by their developmental stage would be found dead in the pre-eyed stage. In essence, the suggestion made is that the compensatory ability of early stage eggs will allow the egg to sustain a stress for a limited time and if the stress is not removed, eventually the egg will die. The delay factor is reduced after a period of approximately 200 degree-days. This is probably synchronous with the establishment of a functioning circulatory system. The limitation imposed by hypoxia on earlier developmental stages tends to fix the embryo in a stage where the response of the embryo is not only greatest in terms of delay in development, but this very response keeps the egg from overcoming its respiratory deficit by not allowing it to get past that critical stage prior to the establishment of a functional circulatory system.

The other main period of mortality, found just prior to hatching (Hayes, 1949), appears to be related to a greater unit-demand of oxygen per egg at a time when the critical demand is high, or where diffusion through the capsule may be limiting the oxygen consumption of the embryo. Pre-hatching stage eggs subjected to decreasing amounts of dissolved oxygen show a progressively earlier hatch from saturation to lower dissolved oxygen levels, culminating in a maximum premature hatch at about 1 p.p.m. dissolved oxygen. If premature hatching is a response to stress from hypoxial conditions then this stress may be present at all levels of oxygen below air-saturation. It would appear, therefore, that pre-hatching eggs reared at oxygen levels approximating air-saturation are limited in their ability to bring sufficient oxygen through the capsule to sustain their normal requirements probably at all levels below air-saturation. It is concluded that any condition in pre-hatching stage eggs tending to limit dissolved oxygen availability will place a stress on eggs which is partially compensated for by premature hatching and escape from the gas exchange limitations imposed by the capsule.

#### CRITICAL DISSOLVED OXYGEN LEVELS

At all stages of development of the salmon egg, the oxygen respired by the embryo must diffuse through a thin enclosing spherical capsule of specified diameter and thickness. Krogh (1941) considers the mechanics of respiration in a spherical body enclosed in a capsule from evidence presented by Harvey. If an homogenous spherical body uses oxygen at a constant rate, and if the



oxygen tension may be assumed to be maintained at zero in the centre of the body:

$$C_o = \frac{A r^2}{6 D}$$

where  $C_o$  = the concentration of oxygen at the surface of the sphere in atmospheres,

$A$  = oxygen consumption of the sphere, in millilitres per gram of total mass per minute (ml./g./min.),

$r$  = total radius of the sphere, in centimetres,

$D$  = diffusion coefficient of oxygen through the capsule, in millilitres per centimetre thickness of capsule per square centimetre of capsule area per minute (ml./cm./cm.<sup>2</sup>/min.).

The formula may be applied to the egg prior to the establishment of a functional circulatory system in order to provide an estimate of the ambient oxygen level required to maintain respiration at a rate independent of the environmental supply. Although the required conditions are not completely fulfilled: viz., the respiring mass is not located in the centre but on the surface of the yolk, the use of this model is considered justified in the absence of better experimental evidence.

When an egg has reached the stage of possessing a functional circulatory system, oxygen diffusing through the capsule is transported to the embryonic tissue with greater efficiency. Again, according to Krogh's models, the tension difference necessary for diffusion of oxygen where its transport is accomplished by blood circulation under the capsule is given by:

$$C_o = \frac{A r T}{3 D}$$

where  $T$  = thickness of the capsule in cm.

$A$  = oxygen consumption of the sphere, in millilitres per gram of larval tissue per minute.

In this case, it is assumed that the oxygen pressure in the perivitelline fluid is zero when the ambient oxygen pressure is at the critical level (see Krogh, 1941, p. 24, for further discussion).

In order to arrive at estimates of critical oxygen levels by these models, a composite has been constructed of the data (see Table IV) with certain data of Wickett and of Hayes. Assuming a value for the diffusion coefficient,  $D$ , of 0.0000123 ml./cm./cm.<sup>2</sup>/min. as found for eggs of the Atlantic salmon at 10°C. (Hayes *et al.*, 1951), thickness of the capsule,  $T$ , for chum eggs as 0.006 cm. (Wickett, unpubl.), 0.29 g. as the weight of chum salmon eggs (Wickett, 1954) and actual egg radii of 0.37 cm. (this paper), estimated critical levels have been calculated by the above formulae. Calculated critical levels are listed in Table V and illustrated in Figure 8.

Values of  $A$ , the oxygen consumption in ml./g./min., have been calculated on the basis of egg weight (0.29 g.) for the period prior to establishment of



TABLE V. Calculation of critical oxygen levels for chum salmon eggs at various stages of development.

Age	O <sub>2</sub> consumption	Computational model	Calculated critical oxygen level	Source
<i>degree-days</i>	<i>ml./g./min.</i>		<i>p.p.m.</i>	
4.0	0.0000055 <sup>a</sup>	Ar <sup>2</sup> /6D	0.72	Wickett (1954)
4.8	0.0000078 <sup>a</sup>	"	1.14	"
48.0	0.0000138 <sup>a</sup>	"	1.67	"
121.2	0.000039 <sup>a</sup>	"	3.96	This paper
162.1	0.0000317 <sup>a, c</sup>	"	3.7	Wickett (1954)
268.2	0.001719 <sup>b</sup>	ArT/3D	5.66	This paper
353.0	0.002006 <sup>b</sup>	"	6.60	"
452.4	0.002185 <sup>b</sup>	"	7.19	"

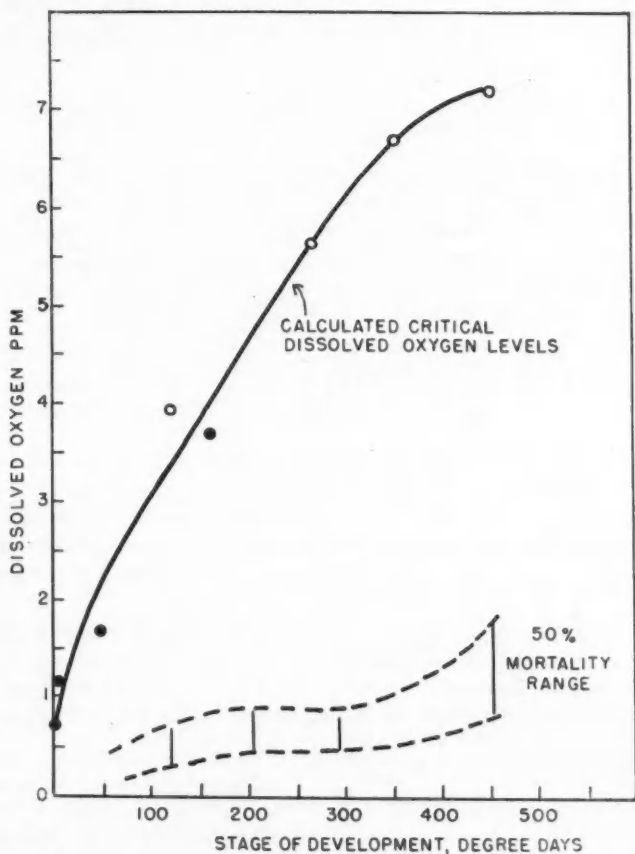
<sup>a</sup>Based on egg weights<sup>b</sup>Based on larval weights<sup>c</sup>Calculated from Wickett (1954), Table I, entry No. 6.

FIG. 8. Estimated median lethal levels of low oxygen and critical dissolved oxygen levels for chum salmon eggs at 10°C. The solid circles represent data for early developmental stages taken from Wickett (1954).

circulation beneath the capsule (estimated at about 200 degree-days) and on the basis of larval weights thereafter (see Table IV).

To illustrate the calculation of critical oxygen levels, the value for eggs at 121.2 degree-days in Table V is obtained as follows. Given  $r = 0.37$  cm.;  $D = 0.0000123$  ml./cm./cm.<sup>2</sup>/min.; and  $A = 0.00093 \times 0.73/0.29 \times 60 = 0.000039$  ml./g./min. where 0.00093 is the oxygen consumption in mg./egg/hr. (Table IV), 0.29 is egg weight in grams and 0.73 is a factor for converting mg. of oxygen/l. to ml. (at 10°C. and 760 mm. Hg.) of oxygen/l.:

$$C_o = \frac{A r^2}{6 D} = \frac{0.000039 \times (0.37)^2}{6 \times 0.0000123} = 0.0723 \text{ atmospheres}$$

Given further that 11.3 mg. of oxygen will dissolve in fresh water at a partial oxygen pressure of 157 mm. Hg. at a total pressure of 760 mm. Hg., the above is equivalent to:

$$C_o = \frac{0.0723 \times 760 \times 11.3}{157} = 3.96 \text{ p.p.m. dissolved oxygen.}$$

Critical oxygen levels are those at which respiratory demand is just satisfied. If these are equivalent to levels below which oxygen uptake is reduced and metabolism and growth decelerated, critical levels are synonymous with limiting oxygen levels (for a discussion of limiting levels, see Fry, 1947, p. 41 *et seq.*). However, as calculated critical levels are partly theoretical in derivation whereas limiting levels may be obtained experimentally, a comparison is necessary to evaluate properly the biological meaning of the former. Unfortunately, the present authors have no information on limiting levels of oxygen for chum salmon eggs capable of comparison. Such information is highly desirable in order to evaluate the significance of critical oxygen levels.

Because of the recognized high oxygen requirements of pre-hatching stage eggs, their susceptibility to mortality and their tendency to hatch prematurely in water of oxygen content below air-saturation, it would appear that critical dissolved oxygen levels may form a basis to denote minimum permissible oxygen levels throughout incubation until more complete information on limiting levels is acquired.

On the basis of experiences encountered with delay in hatching rate caused by imperfect circulation in incubation trays, it is considered appropriate to advocate the use of the recent "vertical" hatchery techniques involving the use of water upwelling through the incubating eggs (see Burrows and Palmer, 1955; Lindroth, 1956).

#### SUMMARY AND CONCLUSIONS

Experiments have been conducted on chum salmon eggs (*Oncorhynchus keta*) in order to investigate some aspects of their response to low oxygen conditions. Eggs at various developmental stages were exposed to a series of low oxygen levels in a constant temperature bath for a period of seven days. Subse-

quently, eggs were cultured under normal conditions until hatching was complete. Observed responses are listed as follows:

1. Oxygen levels below air-saturation at 10°C. produced delay in the mean rate of hatching of eggs tested at four developmental stages. This delay was greatest during early development (between 100–200 Centigrade degree-days) and dropped to lower levels at about the time circulation within the egg was established.

2. In early developmental stages of chum salmon eggs, oxygen levels of 0.3 p.p.m. or less, although not lethal, may result in the production of monstrosities.

3. Eggs of advanced developmental stage are stimulated by low oxygen conditions to hatch prematurely. The peak of premature hatching at 10°C. occurred at an oxygen level approximately equivalent to the estimated median lethal level for dissolved oxygen.

4. The oxygen uptake per gram of larval tissue at 10°C. is high in early development, corresponding approximately to the time of maximum fragility, and falls to a lower value at the end of that period. Subsequently, uptake per gram of larval tissue rises slightly to a level which is more or less constant.

5. Under the experimental conditions, the incipient median lethal level for dissolved oxygen rose with development from approximately 0.4 p.p.m. in early development to 1.0–1.4 p.p.m. previous to hatching.

6. Critical levels of dissolved oxygen were calculated for the present series and compared with values for chum salmon eggs from Wickett (1954). A continuing rise in critical levels is suggested from fertilization at least to a stage shortly before hatching. Until further information is available to the contrary, it is suggested that critical levels of dissolved oxygen may be regarded as a measure of oxygen requirements for successful incubation.

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# Rapid Learning of a Constant Course by Travelling Schools of Juvenile Pacific Salmon<sup>1</sup>

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## ABSTRACT

Either individuals or schools of downstream-migrating chum, sockeye and pink salmon quickly establish a constant course in a circular channel. This clockwise or counter-clockwise course, once established, is not altered by a variety of disturbances including transfer to a channel of different size and shape or, in the case of the chum, removal from the apparatus for almost two days. The schools travel much more frequently in some particular area of a simple maze although, from time to time, they swim through all parts of it. The tendency to swim steadily forward in a winding maze seems to decline as the season of migration comes to an end. Fish trained to swim along one compass direction show no bias for this direction when given a choice of this or an alternate direction at right angles. Fish trained to reverse direction after a definite distance show a tendency to do this when given an opportunity to swim in a channel twice as long. The findings are discussed in relation to simple types of learning such as habituation, insight learning, latent learning and imprinting. The biological significance of the learning is considered in relation to the problem of migration.

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## INTRODUCTION

THE ABILITY TO RECOGNIZE visual patterns and spatial relationships in the environment is found in many groups of animals. Learning based on such an ability enables animals to live within a well-defined home range and, in some cases, to navigate for considerable distances from one territory to another by means of familiar landmarks. Thorpe (1956) has summarized the literature concerning

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this phenomenon in fish. It is well known that fish can be trained to swim through simple mazes and to locate food with respect to different patterns of visual cues. In nature, territorial behaviour, the recognition of a home range, and the return of displaced fish to a particular area have been described by several workers for different species of fish. The learning of spatial relations may play some part in their migrations, but this has not yet been demonstrated. Usually fish navigation based on this ability has been observed to operate only over relatively short distances (home range). Actively migrating species, however, seem not to have been studied in this connection. Further, the available information is almost entirely based on the performance of individual fish or fish which display territorial rather than a schooling behaviour. The present study concerns actively schooling species captured at the beginning of a long migration.

The word "direction" is defined in this study as an orderly "course of movement" whether this is in a straight line or along a curved path. Schools of migrating chum salmon fry (*Oncorhynchus keta*) have been observed to establish constant clockwise or counter-clockwise directions of swimming in circular channels and to maintain these directions for relatively long periods (Hoar, 1956). These directions are established within a few minutes after the school is placed in the quiet water of the circular channel and are not permanently disturbed by light or darkness, by strong avoiding reactions, by changing the location of the apparatus or by excluding direct sunlight. They may be established in a predictable direction by an initial exposure to water currents but the mechanism which maintains the fixed course is unknown.

Several problems arise from this demonstration. One of the most tantalizing of these concerns the significance of this behaviour in the biology of fish. Since the chum salmon is only one of three species of strongly schooling Pacific salmon (*Oncorhynchus keta*, the chum; *O. gorbuscha*, the pink; *O. nerka*, the sockeye) a comparative study might be expected to bring this behaviour into sharper perspective. Another problem concerns the ability of individual salmon to learn such directions. The initial study was based on small schools and this behaviour might be dependent on schooling activity or it might be displayed by individual animals. Finally, we are faced with the question of the nature of the guiding cues. In the original investigation no evidence could be found for any cues responsible for the fixed directions displayed. The present study was undertaken in an attempt to answer some of these questions.

#### MATERIALS AND METHODS

The investigation was carried out at the Port John field station of the Fisheries Research Board of Canada. All fish used were actively migrating. They were taken from a trap placed across Hooknose Creek (chum and pink salmon fry) or Tally Creek (sockeye fry). Chum and pink fry were always studied during the day following the night of their capture. Sockeye fry were studied within one to three days of their capture. The chum fry, at this stage, averaged 37.9 mm. fork length, pink fry 35.1 mm., and sockeye fry 28.1 mm. (Hoar, 1954, 1956).

The circular channels, illustrated elsewhere (Hoar, 1956), are of two sizes. The larger channels are 20 cm. wide and 20 cm. deep with an outside diameter of 120 cm. Thus, the circumference at the centre of the channel is 314 cm. The smaller channels are 10 cm. wide and 15 cm. deep with an outside diameter of 90 cm. and a circumferential distance of 251 cm.

More complex patterns of channels and simple mazes were also used. The maze illustrated in Figure 1 is basically a combination of two isosceles triangles with outer sides 90 cm. long, bounding 15 cm. wide channels within. The triangular channels are connected by two cross channels as shown in the figure. Gates may be inserted or removed at the points indicated by the dotted lines to form pairs of triangles or a large trapezoid, or a trapezoid with a triangular loop on its long side. The latter arrangement forms a series of channels in which the connecting passages change from clockwise to counter-clockwise and vice versa. Straight or curved metal strips could be fixed in the sharply angled corners to form a blunt or rounded wall at the point of turning. The eight different patterns of channels used with this apparatus are shown in Figure 1. For convenience they

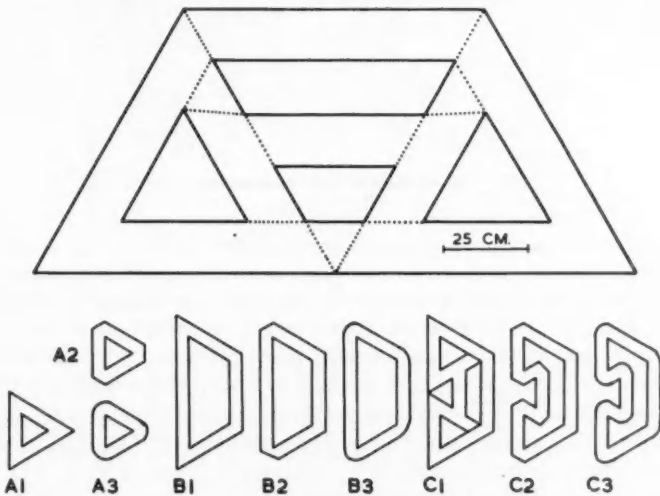


FIG. 1. A maze of channels used to study the learning abilities of pink and chum salmon fry. *Upper*, basic pattern with stippled lines to show the position of gates; *lower*, various patterns of channel used; further description in text.

are referred to as A (triangle), B (trapezoid), and C (trapezoid with loop); and by numbers 1, 2, and 3 to represent respectively the deep, the blunt, and the rounded situation.

With the mazes illustrated in Figure 1 it was never possible to produce a series of curved walls without any irregularities. Ridges, formed where the

metal strips fitted together, interrupted the journeys of the small fish travelling close to the walls and often led to the disorganization of a school of actively swimming fry. The winding channel illustrated in Figure 2 was built to overcome this difficulty. It consists of three small loops and one large one which produce a series of uniform curving channels in which the course alternates from clockwise to counter-clockwise. The channels are 15 cm. wide and 15 cm. deep. The length of the course at the centre of the channel is 585 cm. Other measurements can be obtained from Figure 2 which is drawn to scale.

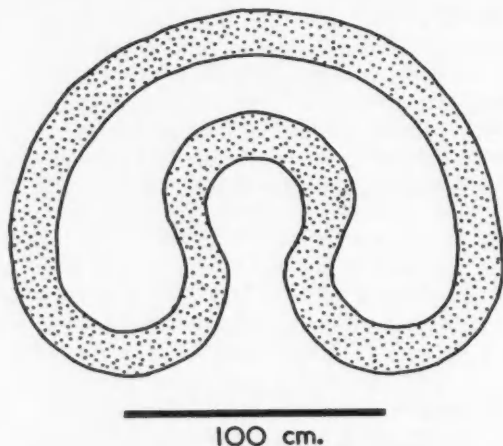


FIG. 2. The winding channel.

An attempt was made to demonstrate the possible learning of compass directions with the apparatus illustrated in Figure 3. This consists of a pair of troughs joined at right angles and a single trough placed beside one of the arms of the angled channel. The length of each channel of the angled trough and the length of the straight trough were the same—235 cm. or just slightly more than sixty times the length of a chum salmon fry. The position of the straight channel was alternated from an east-west to a north-south position in successive tests.

All experiments were performed out of doors. The different channels were placed in the shallow running water of a small tributary of Hooknose Creek and the temperature variations were the same as those encountered by young salmon living under natural conditions in the water surrounding the apparatus. A clump of trees on one side of the stream and a small building about 5 metres distant on the other side may have provided visual reference points. The troughs were emptied and filled with fresh water once daily. Holes in the bottoms of the troughs maintained the level of water at that of the creek. Circular channels were painted with non-toxic "Rustoleum" red paint; the other pieces of apparatus with black asphalt varnish. To make observation easier the bottoms of the channels



illustrated in Figures 2 and 3 were lightly sprinkled with sand. Other general procedures were similar to those previously described. Additional details are given in connection with the different experiments.

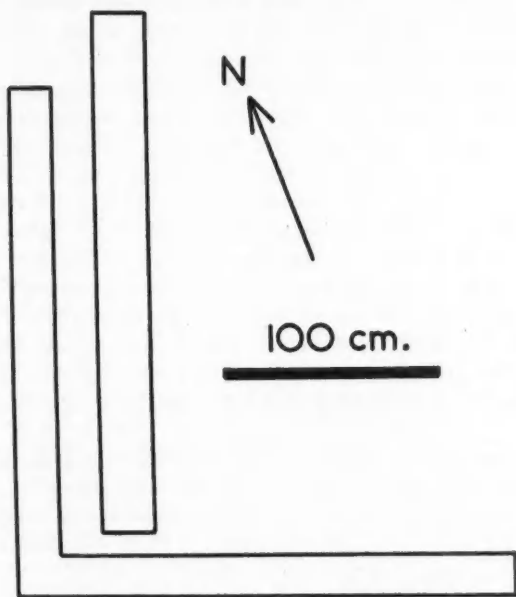


FIG. 3. A straight and a right-angled channel. The arrow shows the north compass direction, which is  $26^\circ$  east of true north. The position of the straight channel was changed in different tests to positions parallel to the bottom arm of the angled channel, which is here referred to as the "east-west" arm.

## RESULTS

### THE BEHAVIOUR OF CHUM SALMON IN CIRCULAR CHANNELS

The earlier description (Hoar, 1956, p. 319) has been supplemented by observing minutely the behaviour of 12 different groups of 25 chum fry when first introduced into the small circular channels.

Initially the chum fry either remain momentarily quiet and then swim off in one or several groups, or they show violent escape behaviour in one locality. If they swim off in a more or less orderly manner, they may make complete circuits immediately—gradually increasing their rate of travel. On the other hand they may make partial circuits moving in different directions or to and fro in a part of the channel. If their initial reaction is to escape, individuals will swim vigorously at the wall of the channel in one locality—occasionally jumping out of the water. This activity persists for several minutes and a few individuals may continue at the same point for as long as an hour.

The escape behaviour was noted when the channels were not uniformly illuminated and strong sunlight played on one side creating a heavy area of shadow on the other. The fish at first usually swam vigorously against the wall in a line away from the sun. In any case, within 1 to 10 minutes, some individuals break away and start circling. With each succeeding circuit, more and more individuals join the travelling school until the group is swimming rapidly around the channel. In the one group displaying the most marked escape behaviour, however, some hesitation was evident even after three hours. As the school came to the point where the escape behaviour was originally initiated, individuals would pause, reverse, and then orient on their established course. Later in the day, when illumination was more uniform and less intense, this activity disappeared.

Quantitatively, 6 of the 12 groups showed the escape behaviour for periods ranging from 2 to 10 minutes. In the other 6 cases, circling was initiated almost immediately (within 1 to 2 minutes). In 4 of the latter groups, the established direction was that which the fish assumed on their first circuit. The entire group may not, in the beginning, circle in an orderly manner. As mentioned above, when a part of the group is set on a definite course, it gradually picks up more and more of the other individuals until the behaviour of the group becomes uniform.

In every case the final direction was established within 12 minutes. The average time required for at least 75% of the individuals to assume a fixed direction of travel was 7 minutes. In the earlier series of experiments (Hoar, 1956), 10 minutes' exposure to flowing water in these channels was sufficient to control the direction established.

#### COMPARISONS OF CHUM, PINK AND SOCKEYE SALMON FRY

Schools of sockeye and pink salmon fry will also maintain a constant course for long periods in the circular channels. The stability of the direction and the regularity of swimming, however, is always less than that observed with schools of chum fry. The pink salmon fry, in particular, regularly show periods of swimming to and fro or of alternating their course. This was unusual with groups of chum fry. Of 94 schools of chum fry studied earlier (Hoar, 1956), only 5.8% altered an established course and only 4.2% failed to establish a definite course. Values for pink fry, studied under comparable conditions, were 22.6% and 13.9% respectively (Table I).

Pink salmon fry travel more rapidly than either chum or sockeye (Table II). The greater activity and marked responsiveness to stimuli may, at least in part, explain the interruptions and irregularities shown by the travelling pink salmon. Confusion results when small detached groups unite with others. The rates shown in Table II are for periods of observation when 75% or more of the school circled continuously and are based on 5 hours of observation of each species divided into 30 different 10-minute intervals. In one hour, pink fry travelled 50 metres farther than chum fry and 150 metres farther than the sockeye fry.

Comparative studies also indicate that the learning is least stable in the

TABLE I. Ability of pink salmon fry to maintain constant directions in circular channel. SC, smaller channels; LC, larger channels.

Series	Schools Size	No.	Duration of test	Schools with direction			
				Constant clockwise	Constant counter-clockwise	Not fixed	Altered after established
SC	25	6	10	4	2	...	2
		6	24	1	5	...	1
LC	20-25	6	10	3	2	1	1
	40-50	6	10	3	3	...	1
	100	3	10	...	3	...	...
	20-25	4	27	1	1	2	1
	50	1	27	...	...	1	...
	100	1	27	...	...	1	...
	50	3	40	1	2	0	1
Total		36	...	13	18	5 13.9%	7 22.6%

TABLE II. Comparison of swimming directions and speed for 6 schools of chum, pink and sockeye fry in 251-cm. circular channels. "Altered": percentage in which direction definitely changed after 2 hours. "Irregular": percentage of observation periods, out of 36, when circling was not continuous by the major portion of the school. "Rate of travel": mean for 30 10-minute periods of observation when travelling was continuous.

	Schools with direction				Rate of travel		
	Clockwise	Counter-clockwise	Altered	Irregular	Av. no. of circuits	Standard deviation	Meters/hour
	no.	no.	%	%	no.		m./hour
Pinks	4	2	33.3	22.2	30.6	7.9	461.9
Chums	3	3	0	5.5	27.2	6.9	411.1
Sockeye	3	3	0	8.3	20.7	3.9	311.6

pink fry. In these experiments, schools were permitted to establish a direction in the 251-cm. circular channels for a period of 10 hours and were then removed to a 10-litre aquarium located at a distant spot under a shelter. They were returned to the circular channels after a period of 10 hours or longer and the direction of swimming recorded (Tables III and IV). In the tabulation of results a chi-square value less than 3.84 indicates that the direction taken by the schools when placed in the apparatus for the second time was a random one, while values greater than 3.84 indicates that the first experience in the apparatus influenced the course which the school took on the second occasion (0.05 point).

It is evident that pink fry showed no ability to assume the original direction when returned after 12 hours. Chum fry, in comparable tests, assumed the same course and the chi-square value for the sockeye fry shows some likelihood (probability about 0.10) that they will also assume the same course when returned after this interval. When isolated for periods of 20 to 40 hours, however, sockeye fry were found to lose the ability to assume the original course while chum fry still maintained the same direction (Table III, Series B). A change in

TABLE III. Comparison of the stability of learned directions in chum, pink and sockeye salmon fry. "Times changed": number occasions when direction altered between tests. "Chi-square": for groups altering direction in total for that species and series.

	Groups tested	Initial direction		Times changed	Chi-square
		Clockwise	Counter-clockwise		
Series A—					
10 to 13 hours between tests					
Chum fry	6	3	3	0	6.00
Sockeye fry	6	1	5	1	2.66
Pink fry	6	2	4	4	0.66
Series B—					
20 to 40 hours between tests					
Chum fry	9	5	4	0	9.00
Sockeye fry	4	3	1	3	1.00

TABLE IV. Stability of learned directions in chum salmon fry. Training period varied from 2 hours (22 tests) to 13 hours; mean, 4.2 hours; "Times changed": number occasions when direction altered between tests. "Chi-square": for groups altering direction in total for that series; first change of direction recorded at 46 hours.

Interval between tests	Groups tested	Initial direction		Times changed	Chi-square
		Clockwise	Counter-clockwise		
10-20 hours	6	3	3	0	6.000
21-40	9	5	4	0	9.000
41-60	21	9	12	9	0.428
Total	36	17	19	9	
46-60	15	6	9	9	

direction was first recorded with the chum fry after 46 hours and Table IV shows that this species "forgets" the established direction after about two days. It is concluded that the stability of this learning, for fish of this age, is greatest in chum fry and least in pink fry.

#### SIZE OF SCHOOL AND DISTANCE TRAVELLED

Experience with schools of pink and chum salmon fry suggested that the order and precision of their travels was dependent upon the size of the group. When one or several individuals drop behind or take a different direction in a small group, they are quickly picked up by the large number of circling individuals. Delays do not occur because a majority of the individuals maintain the course. With smaller groups, separated individuals create delay since there is no large body of individuals to rapidly orient them.

These general observations were quantified by comparing schools of 10, 20, 25, 40, 50 and 100 pink fry and schools of 5, 10, and 20 chum fry. Three large circular channels (314 cm. circumference) could be observed simultaneously. The schools of 10, 20 and 40 pink fry were compared at one time and the groups of 25, 50 and 100 at another. The three different sizes of chum schools were

observed on the same occasions. In each case, the fish were placed in the channels between 9:00 a.m. and 10:00 a.m. and observed 6 times for 10-minute periods at intervals of about 2 hours (60 minutes' observation per group). For each size group, the experiment was repeated 3 times, making a total of 18 observation periods or 3 hours in each case.

Table V summarizes the data for the pink salmon fry. The chum fry values

TABLE V. Effect of size of school on rate of swimming of pink salmon fry. Figures tabulated are the number of circuits of large channels completed in 6 10-minute periods, recorded at 2-hour intervals on the day indicated. Totals are for 3 hours' observation, divided into 18 separate 10-minute intervals spread over three days. Three schools were observed simultaneously in each period.

Date	10	20	School size		50	100
			25	40		
May 9	...	...	51	...	68	90
May 10	...	...	36	...	77	64
May 11	...	...	38	...	94	65
May 12	17	26	...	34	...	...
May 13	55	61	...	70	...	...
May 14	32	60	...	84	...	...
Total circuits	104	147	125	188	239	219
Av. speed (m./hr.)	109	154	131	197	250	229

are given in Table VI. Larger schools travel in a more orderly manner and at a faster rate than the smaller ones. The difference between 5 and 10 chum salmon in the large channels is not considered significant, but the group of 20 has a definite advantage in orderliness.

Observation confirms the quantitative finding that a group of 100 pink fry will not travel as rapidly as a group of 50 fry. There seems to be an optimum size for schooling in these areas. The group of 100 sometimes breaks into several well-organized groups and there are delays when they come together. The precise relationships probably vary with the size of the area in relation to school size. There does, however, seem to be an important general principle that small isolated groups of pink or chum salmon fry will not behave in as orderly and precise a manner as the larger groups.

TABLE VI. Effect of size of school on rate of swimming of chum salmon fry. Figures tabulated are the number of circuits of large channels completed in 6 10-minute periods recorded at 2-hour intervals on the day indicated. Totals are for 3 hours' observation, divided into 18 separate 10-minute intervals spread over three days. Three schools observed simultaneously in each case.

Date	Size of school		
	5	10	20
May 15	87	42	130
May 16	31	23	50
May 17	12	35	55
Total circuits	130	100	235
Av. speed (m./hr.)	136	105	246

# CONSTANT RATES OF SWIMMING BY INDIVIDUAL FISH

It could not be predicted from the foregoing experiments whether or not individual fish would establish and maintain steady directions. The increased precision shown by larger groups suggested that this was a schooling phenomenon. However, the irregularities and slower rates of the smaller groups could be due to confusion resulting from the breaking up of the group and single fish might show the behaviour as markedly as a school of optimum size.

Table VII shows that 1, 2, 3, 4, or 5 chum salmon fry will, in the 251-cm. circumference channels, maintain unaltered directions for long periods with relatively few irregularities. The irregularities recorded (Table VII) show number of 10-minute observation periods when some irregularity such as a temporary reversal or to and fro movements was noted.

TABLE VII. Ability of small groups of chum salmon fry to maintain constant directions in circular channels. Duration of experiments was 12 to 24 hrs., except 5 of single fish at 5-8 hrs. each; observation periods were of 10 minutes. "Altered": percentage in which direction changed after 2 hrs. "Irregular", percentage of observation periods when swimming was not continuous.

Size of group	Different experiments	Total observation periods	Schools with direction			
			Constant, clockwise	Constant, counter-clockwise	Altered	Irregular
			no.	no.	%	%
1	22	95	9	11	2	18
2	2	8	0	2	0	25
3	1	6	0	1	0	33
4	2	8	0	2	0	0
5	1	4	1	0	0	0

Single chum fry were followed for a sufficiently long period (7 hours) to calculate a reliable rate of travel. During 42 10-minute periods when circling was continuous, single chum fry made an average of 28.1 circuits per period. In other words, individuals travelled at the rate of 423 metres per hour. This is slower than schools of 25 chums in the same apparatus (Table XII) and the indications are that the schooling activity of optimum-sized groups stimulates the normal cruising speed. The data were, however, collected under different meteorological conditions and this may account for at least some of the difference.

Five separate tests were made with individual pink salmon fry placed side by side with individual chum fry. The pinks, like the chums, cruised steadily in one direction. In 4 out of 5 of the tests the pink fry did not alter course during periods of 12 to 24 hours. Isolated pink fry always swam slightly more slowly than the isolated chums.

It is concluded from these experiments that individual schooling salmon fry will maintain a steady cruising direction in these circular channels at rates comparable to those of schools of fish.

## ADDITIONAL TESTS FOR THE STABILITY OF THE DIRECTIONS LEARNED IN CIRCULAR CHANNELS

Two additional sets of experiments contributed further evidence concerning the stability of the learning involved in the experiments with circular channels.

In the first series, the interior walls of one pair of the circular channels were differently painted. In one channel, the longer (outer) wall was aluminium coated and the shorter (inner) wall red. The colours were reversed in the other channel. Fish transferred from one channel to the other would be confronted by a different arrangement of colours in the right and left eyes if they continued to travel in the same direction, but the same colour pattern if they reversed directions. Any change in direction or delay in orientation on transfer might indicate that the fish were depending on cues from the channels themselves. Transfer of schools of fish from one channel to the other was made on four occasions. Neither the transfer of the fish nor the shifting of colours on the eyes disturbed the direction initially established.

In the second series, oppositely oriented groups were mixed. These tests were made with 24 chum fry in the small circular channels. Oppositely travelling groups were removed to buckets and 12 of each type placed together in one of the channels. In control experiments, similarly oriented fish were treated in like manner. As might be expected, the mixing of similarly oriented groups produced no confusion or delay.

The results of mixing differently oriented groups of chum fry could not have been predicted from earlier experiments. One of three possibilities was anticipated. The newly grouped fish might, after an initial period of confusion, establish a course in a purely random manner; or if one of the two original groups was more strongly oriented it would set the new course; or the fish might maintain their original directions, resulting in two schools travelling in opposite directions. The latter situation was clearly evident in 3 out of 4 trials and in the fourth, one school remained relatively stationary, while the other swam regularly past and through it.

The two groups remained distinct over a period of 7 hours' observation. Isolated individuals seemed to school temporarily with the oppositely oriented group if they encountered it but would sort themselves out in the confusion which was evident when the 2 groups met. Although this confusion persists only a few seconds, the oppositely oriented groups are definitely delayed on meeting. One group seemed to be more rapid and orderly than the other and in each case this was the group returned to its "home" channel. This type of experiment was not pursued further. The two directions were obvious and in strong contrast to the control experiments. The picture contributed additional evidence for the stability of the learning involved.

#### BEHAVIOUR IN CHANNELS OF DIFFERENT SHAPES

##### 1. A MAZE OF TRIANGLES AND TRAPEZOIDS

In an earlier paper (Hoar, 1954, p. 77), it was noted that chum and sockeye salmon fry will swim back and forth from one end of a 225-cm. trough to the other for prolonged periods. The same kind of constant activity might be expected in any area of quiet water. Circular channels may present a relatively simple situation if the fish are guided by cues in the external environment or, if the established directions are maintained by a "compass mechanism", within the



animal. If, on the other hand, the guiding cues are present in the channels themselves, a slightly less regular environment might provide more guiding stimuli and the fish might readily establish constant directions in simple mazes. This possibility was first investigated with the apparatus illustrated in Figure 1.

It was immediately evident that neither chum nor pink fry could establish an orderly direction when confronted by the deep angles (situation 1, Figure 1). They regularly entered these corners (seemingly "culs-de-sac"), milled about, and either swam back along the same channel or moved in an unpredictable manner through the apparatus. Swimming to and fro in one, or perhaps two, of the channels was more frequently observed than random movement through the channels. Individuals are evidently able to apprehend these spatial relations ("insight") for, although in a series of observations they will be found to explore all of the different channels, they are most frequently found in only one or two of them.

Quantitative data are shown in Table VIII. In these experiments, two groups of 50 pink fry were observed at the same time in a pair of trapezoids with open

TABLE VIII. Position of pink fry schools with respect to different areas of trapezoids with loops, May 10, 1956. Series I, apparatus C1; Series II, apparatus C2 (Fig. 1). Positions were recorded at 30-second intervals for 20 times throughout the day as indicated. 50 fish were in the channels; further description in text.

Area No.	Times recorded in areas							
	1	2	3	4	5	6	7	8
Series I								
11:00 a.m.	16	1	...	...	...	...	1	6
1:00 p.m.	10	12	...	...	...	...	...	1
2:00 p.m.	14	7	2	6	1	1	...	1
5:00 p.m.	20	1						
6:00 p.m.	20	4						
7:00 p.m.	20	...						
Series II								
11:00 a.m.	4	4	3	1	3	3	4	9
1:00 p.m.	...	1	1	3	3	5	11	3
2:00 p.m.	...	...	...	...	...	...	...	20
5:00 p.m.	...	...	...	...	3	3	3	17
6:00 p.m.	...	...	...	...	...	...	1	20
7:00 p.m.	...	...	...	...	...	...	2	20

triangular loops (situation C in Fig. 1). One trapezoid (first series of data, Table VIII) had deep angles, while the angles were blunted in the other. The channels were numbered consecutively, starting in a clockwise direction with the shorter of the two parallel sides (top, Fig. 1). At each time of observation, the position of the major portion of the school was recorded 20 times at 30-second intervals. It is evident that, for a full day, one group preferred channel 1 and the other channel 8. Each group frequently travelled along one of the neighbouring channels and was occasionally seen in all channels. The preference for and recognition of a definite area, however, seems definite. Some apprehension of the area must be involved.



When the corners are blunted (situation 2, Fig. 1) the fish move more freely from one channel to another. In the above experiment several complete circuits were made during the first two observation periods. With the bluntly angled trapezoid B, complete circuits were frequent. However, individuals regularly lose contact with the main school at the angles and circling is never maintained for any prolonged period, nor is the direction constant.

When the corners were rounded (situation 3, Fig. 1), groups of chum fry often circled freely and maintained the established direction for many hours. In 3 out of 4 of the tests with rounded triangles, the direction was definite after 12 hours but by 24 hours only 1 of the 4 groups was circling in the original direction. In trapezoids with rounded corners, 3 of the 7 schools showed a constant direction of circling for periods of from 1 to 7 hours. Thereafter, they failed to swim in one direction and usually showed to-and-fro activity in one area as described above. Untrained fish never maintained a constant direction in trapezoids with loops (C arrangement, Fig. 1). Thus, the behaviour in the various modifications used with this apparatus never shows the precision demonstrated in the circular channels.

The behaviour in triangles and trapezoids with rounded corners is, however, quite predictable. Schools when first introduced swim freely and rapidly around the apparatus. The alarm stimulus associated with moving seems to stimulate them to swim rapidly forward. Later, however, individuals delay more and more when encountering irregularities in the walls of the channels (lines of contact for corner pieces). Eventually, circling ceases and a smaller segment of the environment is occupied.

Circling was never as orderly or as rapid in triangles and trapezoids with rounded corners as it was in the circles. Delays and the eventual disorganization of the direction appeared to be related to the abrupt transitions from straight to curved walls or to the projecting strips which hold the gates in place.

## 2. WINDING CHANNELS

One effort was made to develop a tortuous channel with uniformly curving smooth walls. Groups of 25 pinks or chums were studied in this channel (Fig. 2) for periods of from 10 to 48 hours and careful charts made of their journeys.

Sometimes the initial response during the period of intense excitement following transfer to the apparatus was to swim steadily forward and to make several uninterrupted journeys through the maze. Just as often, however, the initial course seemed haphazard with the entire school or several small groups travelling for a while in one direction and then in another.

Qualitatively the observations failed to show any evidence of improved performance while in the channel. After one day or after one hour, the school might journey steadily on through the maze or it might change direction frequently. The course was usually altered in the middle loop (Fig. 2), less frequently on the end curves and rarely on the long arc. When the school arrived in the middle loop it often slowed down and, after hesitating, appeared to take a random direction. This sometimes happened in the end curves, but the most

obvious feature of the whole series of observations was the hesitancy and alteration of course in the middle loop. Only one group of fish (chums, May 9, Table IX) swam steadily on one course for a full day and this group repeated the demonstration when tested again after removal from the apparatus for 24 hours. Pink fry never maintained a constant course from one observation period to the next.

The quantitative data are presented in Table IX. Periods of observation were for 10 minutes at intervals of from 2 to 3 hours. Eight groups of chums and 3

TABLE IX. Behaviour of salmon fry in winding channel (Fig. 2). "Steady circuits": number of circuits counted when at least 75% of the group was swimming continuously forward three or more times through the maze. "Direction": number of 10-minute observation periods when course did not alter (steady) or was "irregular". Schools were of 25 fish each. An asterisk indicates the only group (see page 263) maintaining constant course from one observation period to the next; further description in text.

Group	Time in channel	Observation periods	Steady circuits		Direction	
			Total	Per period	Steady	Irregular
<b>Chum Fry</b>	<i>hours</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>
May 9*	24	5	42	8.4	2	3
11*	12	7	51	7.3	4	3
10	10	4	3	0.8	0	4
12	12	5	11	2.2	1	4
14	12	6	31	6.1	0	6
16	12	3	11	3.6	0	3
18	14	5	5	1.0	0	5
20	48	12	12	1.0	1	11
22	24	6	3	0.5	0	6
Total	168	53	169		8	45
<b>Pink Fry</b>						
May 13	12	7	42	6.0	3	4
15	12	6	32	5.3	4	2
17	12	5	23	4.6	0	5
Total	36	18	97		7	11

groups of pinks were studied. Chum fry maintained a constant course during 8 of the 53 observation periods (15%). Although the data for pink fry are fewer (18 periods with 3 groups) their performance seemed somewhat better (39%). However, in most of the observation periods with both species the course was altered frequently in what seemed to be a random manner. Quantitatively the data, based on the total of courses completed, shows that the chums travelled more than twice as often along a particular course (clockwise direction on the long arc) while the pinks travelled three times as often in the opposite direction. These findings are considered fortuitous and if the data for pinks and chums are combined the chi-square value is 1.375 (352 journeys completed) indicating small chance that the direction is other than random.

The data were examined in another way. If more than 75% of the members of the school travelled steadily forward for three or more complete journeys

through the winding maze, the course was considered to have some constancy of direction. The number of these journeys has been totalled, recorded in column 4 of Table IX and related to the total number of observation periods (Column 5). These data suggest a change in the performance of the fish during the course of the study. Unfortunately, stocks of fish were not available for additional observations on this point but with both pink and chum fry the number of continuous journeys declined in later experiments.

It is suggested, in a tentative way, that this is a measure of decreasing "internal motivation" (Thorpe, 1956) in these migrating fish. The possibility of such a decline has been discussed elsewhere (Hoar, MS) and reference made to the observation that after mid-May at Port John the chum fry rise more often to the surface for food particles and school less actively. By mid-May in 1957—when the experiments recorded in Table IX were performed—the chum and pink salmon migrations had passed the climax in Hooknose Creek. The peak of the pink migration was between April 27 and May 1 with 35,000 to 50,000 pink fry passing into the sea each night. By May 5, this number had declined to 12,000; by May 10 to 3,000. After May 15, fewer than 500 pink fry passed through the traps nightly. The chum migration reached a peak between April 30 and May 4 with 5,000 to 10,000 fish nightly. By May 10 the numbers were fewer than 1,500 and by May 15 only about 500 fish nightly. Thus, the number of migrants in the river was declining rapidly when these observations were made. The decreasing precision of the course in the winding channel parallels the decline in number of migrants whether or not there is any real correlation in the "internal motivation".

#### EFFECT OF PRIOR TRAINING IN CIRCULAR CHANNELS ON THE BEHAVIOUR IN A MAZE

The stability of the direction learned in the circular channels was next studied by transferring schools from circular channels to triangles and trapezoids (Fig. 1). Several critics had suggested that the ability of chum fry to maintain stable directions in circular channels was due to a "memory" of the spatial relations of the inner and outer arc of the circle. If this is true, prior experience in a circular channel would not be expected to influence the direction of swimming by schools transferred to channels of different sizes and shapes such as the triangles or trapezoids. If, on the other hand, the fish are guided by external cues or if they possess some kind of an "internal compass" a period of activity in a circular channel might introduce a bias in the direction of swimming through a simple maze.

Schools of 30 chum fry were first placed in the large circular channels for periods of 2 to 4 hours (14 tests); 6 to 7 hours (18 tests); 15 hours (2 tests); and 24 hours (3 tests). The minimum period was sufficient to establish a direction which (Table IV) would be "remembered" for at least 46 hours while isolated from the apparatus.

Table X shows that the direction learned in the circular channel is regularly resumed when fish are transferred to channels of other shapes. With prior experience in circular channels, the schools may even navigate many times

TABLE X. Directions of chum and pink salmon fry in triangular mazes. "Direction": number of schools which made continuous complete circuits for 10 minutes or more. "Trained": groups with previous experience in large circular channels. An asterisk indicates that the schools sometimes completed several continuous circuits, but in a disorderly manner, and their direction was not maintained from one period to another.

Pattern	Size of School	Pink fry		Chum fry			
		Tests	Direction	First experience		Trained	
				Tests	Direction	Tests	Direction
A1	12	4	0	...	...	...	...
	25	3	0	10	0	...	...
	50	3	0	...	...	...	...
	100	1	0	...	...	...	...
	200	1	0	...	...	...	...
A2	25	...	...	...	...	2	1
A3	25	...	...	4	3	...	...
B1	50	2	0	1	0	...	...
B2	20	...	...	...	...	1	1
	30	...	...	4	0*	3	3
	50	2	0*	1	0	...	...
B3	30	...	...	7	3	16	13
C1	50	3	0	1	0	...	...
C2	50	3	0	1	0	...	...
C3	30	...	...	6	0	14	9

through the maze of channels in the trapezoids with loops (situation C3, Fig. 1). In every case, however, the activity ceases after 2 to 6 hours. A few individuals first delay at an angle on the wall of a channel. Reversals become progressively more frequent until the original direction is no longer evident and the group remains for longer periods in some particular channel—eventually behaving the same way as the untrained fish.

That the direction learned in the circular channels is applied to channels of other shapes was clearly evident in the trapezoids with loops. The direction from which the fish entered the loop depended on the direction of movement in the circular channel. Even when they failed to navigate the loop, they persistently and repeatedly entered it from one side. Within the loop, they regularly made the first ("wrong") turn—contrary to their learned direction—but hesitated on the second one which would take them fully around in an opposite direction. One of three things was then observed. A school might make the second turn and continue through the apparatus for a time, showing improvement in the speed and regularity of travel; or the school might mill at this point and turn back; or it might cross to the opposite side of the channel and complete a circuit in the established direction (reversing direction through the maze).

It was concluded from these experiments that the cues which guide chum salmon in their circular channels are not dependent upon the shape of the channels. The circular channel, because of its uniformity, permits the expression of an ability which either depends on cues in the external environment or is rapidly fixed in the neuromuscular system by prior experience.

#### CONSTANT DIRECTIONS IN STRAIGHT CHANNELS

In the next experiments, fish were permitted to swim back and forth in either an east-west or a north-south direction and then given the opportunity of a choice of direction in a pair of connecting channels set along opposite compass lines (Fig. 3). Such a test might be expected to show whether the fry could maintain a compass direction and/or were being guided by cues outside of the channels.

Groups of 25 chum fry were placed for 24 hours in the straight channel and then transferred to the angled apparatus. The fish had been captured the previous morning and were placed in the trough or transferred to the angled channel at 6:00 a.m. Control groups were introduced directly into the angled apparatus without experience in any of the different patterns of channels. Ten-minute records of the journeys of the schools were made at 7:00 a.m., 8:00 a.m., 9:00 a.m., 10:00 a.m., 12:00 noon, 3:00 p.m., and 6:00 p.m. This is a total of 7 observation periods or 280 minutes for each group. Four groups of controls and 4 groups of experimentals for each of the 2 trough directions were studied in this way. There were 2 other control groups with 5 periods of observation instead of the usual 7.

The control fish usually swam the entire course of the angled channel, travelling freely around the angle without any evidence of hesitating. The relatively wide angle seemed to provide an open stretch of water into which the rapidly travelling school swam far enough so that no sharp choice was required. In the 6 groups observed (total 380 minutes' observation) the schools (75% or more of the individuals) approached the angle 454 times and on 358 occasions (79%) the choice was to continue the journey into the next channel. In 96 cases the groups reversed and went back to the end from which they had started. Several of these cases of frequent reversing were related to strong sun on one channel and deep shadow on the other. On the 96 occasions when the groups were reversing to the original direction, 57 were in the north-south channel and 39 in the east-west channel (chi-square 3.583) suggesting a bias for the north-south channel. This channel was shadowed during the strong afternoon sunlight.

These control experiments show that there is little or no preference for one or other of the arms of the channel and that the usual behaviour is to swim from end to end of the apparatus without any evidence of making a choice at the angle.

In the groups trained to a general north-south direction (4 tests), there were 269 occasions when the schools approached the angle and 136 occasions (50.5%) when they chose to continue the journey. The behaviour was regularly different from that of the controls—at least after the initial alarm reaction. When the experimental groups arrived at the angle they slackened speed and instead of swimming steadily into the next channel hesitated and appeared to reorient on a random course. The values of 133 reversals to 136 continued journeys substantiates this and suggests that the previous training has influenced their behaviour. There is a tendency to stop swimming after a certain distance or a

certain time and to take a random course. The channel selected, however, bore no relation to the direction of the channel in which they had been trained. Of the 133 cases mentioned above, 64 were in the north-south direction and 69 in the east-west direction.

The results with groups having prior experience in the east-west channel were less consistent but still regularly different from the controls. In this case 328 choices were recorded in the same number of groups and observation periods. Of these, 210 were to continue and 118 to return to the same channel. The chi-square value of 12.903 indicates a strong likelihood for the group to continue rather than to reverse direction. However, in the control experiments the groups continued their journeys in 79% of the cases, while those in the present experiment continued 64% of the times. In this case, the preference was definitely for the north-south channel (82 to 36) which, as in the case of the controls, was the area of strong shadow during the intense afternoon light. Fortunately, cloudy and rainy weather prevailed during most of the period of study but this was not always the case.

Qualitatively, it was evident that the alarm associated with transfer of the fish stimulated both trained and untrained fish to swim as far as possible at the beginning of the experiment. Thereafter, during a period of about 3 to 5 hours the behaviour of the experimental groups was different from that of the controls. After this time, however, they appeared to be adapted to the new area. Reactions were compared at the different times of the day in an attempt to eliminate some of this variability introduced by the initial excitement and the gradual conditioning to the new area. Only the 4 control groups in which times of observation were strictly comparable to those of the experimentals were included in the comparison. The data summarized in Table XI are variable but it is evident that, with 3 exceptions in 14 comparisons, the choice to continue the journey was made a greater percentage of the times by the control than the experimental groups.

In summary, these experiments provided no evidence that the fry are guided in the channels by means of cues in the world outside the channels, but suggest strongly that they can be trained to swim for a certain distance or a

TABLE XI. Behaviour of chum salmon fry in a right-angled channel (Fig. 3). "Choices": total number of times during 40 minutes that the school swam into the junction of the two arms. "Continued": percentage of this number when the journey continued into the other channel. Data are based on 4 groups, each observed 10 minutes at the time indicated; further description in text.

	Control		Trained North/South		Trained East/West	
	Choices	Continued %	Choices	Continued %	Choices	Continued %
7:00 a.m.	69	95.6	48	51.1	55	80.0
8:00 a.m.	59	62.7	40	50.0	50	40.0
9:00 a.m.	39	79.5	28	60.7	45	55.5
10:00 a.m.	51	58.8	33	63.6	38	65.6
12:00 noon	39	69.2	43	37.2	44	59.1
3:00 p.m.	43	88.4	35	31.4	46	67.8
6:00 p.m.	43	76.7	42	66.6	40	97.7

definite time without any reward other than the freedom to swim. Further explorations along this line would have to be made under controlled laboratory conditions. The variations in light and temperature and the many disturbances in the "out-of-doors laboratory" were responsible for some of the variability in results. It should not be difficult to demonstrate the presence of some kind of a distance or timing mechanism in these fish.

#### RATES OF TRAVEL IN CHANNELS OF DIFFERENT SHAPES

The rate of swimming may be expected to vary with temperature of the water and the time of the day. Chum salmon fry, studied in the straight 225-cm. troughs (Hoar, 1954), travelled at rates varying from 85.5 metres per hour ( $10^{\circ}$  to  $13^{\circ}\text{C.}$ ) to 198 metres per hour ( $13^{\circ}$  to  $17^{\circ}\text{C.}$ ). Diurnal fluctuations have been described (Hoar, 1956). It seems also that the precision is greater in the narrow circular channels where isolation and reversals of small numbers of individuals are at a minimum.

Quantitative data (Table XII, A) are available for schools of chum salmon observed *at the same time* in small and large circular channels and in trapezoids with rounded corners (previously trained fish). It is evident that the distance travelled per unit time depends on the shape and width of the channel. In these experiments, distances travelled by schools of the same size and in the same channels were greater than those recorded in Table II. The fish described in Table XII, A, were 2 weeks older and the water temperature had risen from a midday maximum of  $9.5^{\circ}$  to  $12.5^{\circ}\text{C.}$

Groups of 25 pink fry or 25 chum fry were also compared in the straight and the angled channels shown in Figure 3. Duplicate experiments were carried out with both pinks and chums. The results (Table XII, B) show that the rate is considerably greater in the longer channel where the fish do not reverse directions so frequently and that, in these groups, the chums swam much faster than the pinks (compare Table II).

TABLE XII. Rate of travels of schools of fry (20 to 25 individuals) in channels of different shapes. Measurements made at same times. Series A, May 21 to May 24, 1956; Series B, May 10 to May 15, 1957.

Apparatus	Observation time	Rate
Series A	<i>min.</i>	<i>m./hr.</i>
Chum fry		
Circular channels		
(251 cm. circumference)	78	636
Circular channels		
(314 cm. circumference)	87	542
Trapezoids with rounded corners B3		
(358 cm. distance)	150	358
Series B		
Chum fry		
Straight channel	50	117
Right-angle channel	50	141
Pink fry		
Straight channel	90	80
Right-angle channel	90	99



## DISCUSSION

These observations confirm the earlier report that chum salmon fry quickly learn a constant course of travelling in circular channels and show that the pink and sockeye fry have a similar ability. During the course of this study, several other simple learning processes were evident in the salmon. Chums and pinks readily recognize specific areas of a complex maze of channels and return to these repeatedly. There is also a strong indication that the chum fry may be able to apprehend a definite distance or a time of travelling. All these examples involve a learning without patent reward. These activities of the salmon fry are of biological interest not only as simple learning processes but also as mechanisms of possible significance in the life of animals which are commencing a long journey from which they are highly liable to return to the same region. The nature of the learning processes will be discussed before considering the possible significance of these activities in the life of the salmon.

## THE NATURE OF THE LEARNING

The instinctive behaviour of the juvenile Pacific salmon has been described in some detail (Hoar, MS). The basic behaviour pattern under observation in the present experiments is the active schooling of young salmon in quiet water. At this stage in life, their normal behaviour in quiet water is to school and swim actively. In experimental situations such as used here the only obvious orienting factors are the walls of the channels. The active swimming is classed as appetitive behaviour and may involve both escape and exploration on the part of the fish.

Thorpe (1956) describes a fundamental relationship between escape and exploratory behaviour in animals. Thus, he writes "a new stimulus that is very intense provokes flight, whereas a similar stimulus of lesser intensity releases cautious investigation which slowly decreases the intensity and unfamiliarity of the stimulus and so leads to habituation. Thus fear reactions and exploratory reactions are evoked by the same stimulus at different intensities."

Escape behaviour was manifest in these experiments by the initial persistent swimming at the wall of the channel or by the more rapid rate of travelling always noted when fish were first introduced into the strange environment. After a time the schools swim to and fro in a trough or cruised around the channels at relatively constant rates for many days. The disappearance of the escape behaviour is clearly a matter of habituation (Thorpe, 1956). It may be of interest that in some situations, habituation does not occur and escape behaviour persists. For example, larger schooling fish (sockeye salmon smolts) when placed in a relatively narrow vertical tank where they cannot swim forward for any considerable distance will show escape behaviour for several days (Hoar, Keenleyside and Goodall, 1957).

The exploratory activities of juvenile schooling salmon have been described (Hoar, 1954, p. 77). This behaviour is probably often involved in the activity which these fish show in the many channels of the mazes and in the circular channels. In the former case the fish, although preferring one area, do occasion-



ally swim through all the channels; in the latter case, the motivation to explore may be coupled with the behaviour of constantly swimming in quiet and relatively shallow water.

Several learning phenomena may be superimposed on the basic behaviour described above. *Habituation* has already been mentioned and is probably manifest in a number of ways when the fish gradually become more familiar with the strange environments in which they are placed. *Insight* or apprehension of spatial relations, may have been evident when the schools of chum and pink fry were studied in the triangular maze and found to relate their activities to a specific area although exploring the entire pattern. Hasler (1956) found that *Phoxinus* was able to obtain reference points from small imperfections in the wall of a tank which were not evident to man and this may also have been the case in these experiments. However, this factor was eliminated in the experiments with circular channels by transferring fish from one channel to a differently painted and differently sized channel, by transferring them from circular channels to the simple mazes and particularly in the experiments with the right-angled channel by training the schools first in a different channel. In each case some evidence of the prior experience was seen after the transfer. Some apprehension of spatial relations (insight) seems evident with the juvenile schooling *Oncorhynchus* but the experiments provide no evidence for insight learning or a new adaptive response as the result of insight (Thorpe, 1956).

The learning of constant directions in circular channels has many of the characteristics of *latent-learning* as described by Thorpe (1956). Latent-learning is based on or results from exploratory behaviour and is inseparably tied up with insight. The term was coined to denote learning without patent reward—"the association of indifferent stimuli or situations without patent reward" (Thorpe, 1956). On the other hand, the activity described here has some of the characteristics of *imprinting* in that it is an extremely rapid and superficially unrewarded type of learning. However, unless it can be shown to be characteristic of and confined to a brief period in the animal's life and until there is more knowledge concerning the reward, it lacks the essentials of classical imprinting. The only reward apparent in this situation is "uninterrupted swimming". The fundamental behaviour is to constantly swim and this can only be realized when the direction does not vary. This is learned rapidly.

The cues involved in maintaining the direction in spite of many disturbing situations have not been demonstrated. The fact that the apparatus can be covered or may be moved from one place to another argues against celestial reference points such as have been demonstrated for several species of migrating or homing animals (Frisch and Lindauer, 1954; Hasler, 1956; Matthews, 1955). Celestial reference points, however, have not been excluded in the experiments with circular channels if it is assumed that momentary observation of the sky—even though clouded—could orient the travels for many hours. It has been possible to exclude visual cues from imperfections in the walls of the channels such as Hasler (1956) described for *Phoxinus*.

Since no environmental guiding cues have been found in this long series of

tests, one may be justified in considering an alternative hypothesis. It is suggested as a tentative explanation that the experiences of swimming steadily forward in a circle or of travelling to and fro along a straight line for a definite distance in some way modify the neuromuscular mechanisms of the animal. In the first case the tendency is to turn to the right or the left—as in the inherent tendency of man to operate with the right or left hand. In the second case, the tendency is to act in specific manner for a fairly constant period of time. Such rhythms are not unusual in the animal world. Mechanisms of this type may be highly important to the salmon.

#### BIOLOGICAL SIGNIFICANCE OF THE LEARNING PROCESSES

It should be emphasized that the young salmon studied here were captured at the beginning of a long migration into the Pacific Ocean from which many will return rather precisely to the same area. At the moment of capture and perhaps for some weeks after entering the ocean their journeys may be directed by the flowing waters of streams or by the shores of the estuaries and neighbouring coast. However, within a short time, Pacific salmon are found swimming far out in the ocean, at great distances from their natal streams. It now seems unlikely that they are behaving as planktonic individuals and the alternative theory is that mechanisms are available for precise navigation over long distances.

Adequate mechanisms for such navigation have not yet been demonstrated. The fish must, of course, be guided in their journeys by environmental cues which are related in a precise and reliable fashion to their goal. These environmental cues must, moreover, stimulate receptor organs and be perceived by the fish. The essential problem remains one of relating environmental cues to sensory mechanisms.

An activity adhered to as stubbornly as that shown by the young salmon maintaining a steady course in the circular channels may be assumed to be of importance in the life of the salmon. It seems logical to attempt to relate it to migratory behaviour. Such an ability does not appear to be required for downstream migration (Hoar, MS). In this case the basic mechanisms are active swimming and schooling at low light intensity in the presence of such environmental directing factors as the flowing water. In any case the direction of downstream migration is a most variable one in different rivers but fixed for any particular school of fish by the geography of the river. If then, the behaviour is of biological significance in migration it must be a behaviour—possibly in the process of ontogeny—which will be expressed in the ocean travels.

This learning may, however, be of importance to the animal but play no particular part in its migratory activity. The schooling reaction of fish is a complex behaviour pattern and the ability to turn constantly in one way might be a part of it. A comparative investigation of this learning in a variety of schooling fish—both migratory and non-migratory—should assist in an evaluation of its significance. Some preliminary experiments have shown that sand lance (*Ammodytes tobianus personatus*) behave like the young salmon schools, while small schools of sea perch (*Cymatogaster aggregatus*) and tube snout (*Aulorhynchus*

*flavidus*) swim back and forth at one side of a circular channel and do not swim constantly around it. The coho fry (*Oncorhynchus kisutch*) behaves more like the last two species even though it may school actively under certain conditions (Hoar, MS). This learning does not seem to be a characteristic of all schooling fish.

#### SUMMARY

1. A stable course of swimming in circular channels is established by chum fry in 10 minutes or less.

2. In circular channels, pink and sockeye salmon fry will also swim for long periods in one direction.

3. Chum salmon fry will swim in the original direction when returned to the circular channels after having been removed from them for 48 hours; sockeye fry for only 24 hours and pink fry for less than 12 hours.

4. Of the three different species of schooling salmon fry, recently emerged pink fry travel most rapidly in the circular channels and sockeye most slowly. The rates, however, vary with the size of the school and the dimensions and shape of the apparatus.

5. In circular channels, individual chum and pink salmon fry swim in constant directions at rates comparable to those of optimum-sized schools.

6. Schools of chum and pink salmon fry will explore all parts of a maze of channels but soon show a marked preference for some particular area where they swim to and fro for long periods.

7. Chum fry, when trained in circular channels, maintain the same direction in a trapezoid or in a simple maze where the direction changes from clockwise to counter-clockwise or vice versa. The behaviour, however, is less orderly and, after several hours, the fish select some particular area of the apparatus and school to and fro in this area.

8. Two groups of chum salmon fry, trained to swim in opposite directions, will maintain these directions when the two groups are mixed in equal numbers.

9. Behaviour in a winding maze of channels suggests that the tendency to swim steadily forward declines as the season advances.

10. Fish trained to swim along one compass direction do not later show a preference for this direction when given the alternative of this or a direction at right angles to it.

11. Fish trained to reverse direction after a definite distance (time) will show a tendency to do this when given an opportunity to swim twice as far before turning.

12. The learning involved in continuously swimming clockwise or counter-clockwise in the circular channels is not dependent on visual cues from the walls of the channels nor has it been related to factors in the external environment.

13. Habituation and insight are evident in the learning processes involved and the rapid learning of a constant direction in circular channels was considered in relation to latent learning and imprinting.

14. The learning demonstrated may be of significance in the oceanic migrations of the species.

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